Physiological aspects of the fish-to-tetrapod transition – skin structure, breathing and feeding in early tetrapods

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Dermal bone sculpture in early tetrapods: external morphology, histology and possible functions

[1] Witzmann, F., Scholz, H., Müller, J. & Kardjilov, N. 2010. Sculpture and vascularization of dermal bones, and the implications for the physiology of basal tetrapods. – Zoological Journal of the Linnean Society 160: 302–340.

[2] Witzmann, F. 2009. Comparative histology of sculptured dermal bones in basal tetrapods, and the implications for the soft tissue dermis. – Palaeodiversity 2: 233–270.

[3] Janis, C. M., Devlin, K., Warren, D. E. & **Witzmann, F.** 2012. Dermal bone in early tetrapods: a palaeophysiological hypothesis of adaptation for terrestrial acidosis. – Proceedings of the Royal Society of London, Series B 279: 3035–3040.

[4] Witzmann, F. 2010. A skull fragment of a Devonian tetrapod in the collection of the Museum für Naturkunde Berlin showing a unique lateral line morphology. – Fossil Record 13: 297–302.

Osteoderms (dermal armour plates) in early tetrapods

[5] Witzmann, F., Schoch, R. R. & Maisch, M. 2008. A relict basal tetrapod from Germany: first evidence of a Triassic chroniosuchian outside Russia. – Naturwissenschaften 95: 67–72.

[6] Witzmann, F. & Soler-Gijón, R. 2010. The bone histology of osteoderms in temnospondyl amphibians and in the chroniosuchian *Bystrowiella*. – Acta Zoologica (Stockholm) 91: 96–114.

[7] Buchwitz, M., **Witzmann, F.**, Voigt, S. & Golubev, V. 2012. Osteoderm microstructure indicates the presence of a crocodylian-like trunk bracing system in a group of armoured basal tetrapods. – Acta Zoologica (Stockholm) 93: 260–280.

Structure of dermal scales in early tetrapods and their fish-like relatives

[8] Witzmann, F. 2007. The evolution of the scalation pattern in temnospondyl amphibians. – Zoological Journal of the Linnean Society 150: 815–834.

[9] Witzmann, F. 2011. Morphological and histological changes of dermal scales during the fish-to-tetrapod transition. – Acta Zoologica 92: 281–302.

The hyobranchial apparatus in early tetrapods and its significance for feeding and breathing

[10] Witzmann, F. 2013. Phylogenetic patterns of character evolution in the hyobranchial apparatus of early tetrapods. – Transactions of the Royal Society of Edinburgh 104: 145–167.

[11] Schoch, R. R. & **Witzmann, F.** 2011. Bystrow's Paradox: gills, fossils, and the fish-to-tetrapod transition. – Acta Zoologica (Stockholm) 92: 251–265.

[12] Witzmann, F. & Schoch, R. R. 2013. Reconstruction of cranial and hyobranchial muscles in the Triassic temnospondyl *Gerrothorax* provides evidence for akinetic suction feeding. – Journal of Morphology 274: 525–542.

[13] Witzmann, F. & Schoch, R. R. 2006. Skeletal development of the temnospondyl *Acanthostomatops vorax* from the Lower Permian Döhlen basin of Saxony. – Transactions of the Royal Society of Edinburgh: Earth Sciences 96: 365–385.

ABSTRACT

This habilitation thesis seeks to contribute to the knowledge of the physiology and way of life of early tetrapods of the Palaeozoic and Mesozoic. It is based on 13 included papers and focuses on the evolution of skeletal correlates from which the integumentary structure and the mode of breathing and feeding can be inferred.
The first part of the thesis is composed of morphological and histological investigations of dermal ossifications in a wide range of early tetrapods. Dermal bone sculpture contributed to the consolidation of a dense integument; this and numerous dermal ossifications like osteoderms (armour plates) and scales render substantial cutaneous respiration as in extant lissamphibians unlikely. It is hypothesised that a further function of dermal bone sculpture was to buffer CO_2-induced acidosis while the animals were on land. Numerous early tetrapods independently developed osteoderms in the trunk that may have served among other things for support of the vertebral column in terrestrial locomotion, buoyancy in aquatic forms and as a physiological calcium reservoir. The alterations in morphology, histology and arrangement of dermal scales during the fish-to-tetrapod transition occurred at roughly the same time when digits appeared and enabled greater flexibility of body and limbs. The second part of the thesis is concerned with the hyobranchial apparatus (or gill skeleton) and its role in breathing and feeding in early tetrapods. The fish-like hyobranchium was retained in an unexpected large number of early tetrapods, showing that many early tetrapods of both the stem- and crown-group breathed via the associated internal gills as adults, and via external gills as larvae. The hyobranchial apparatus and reconstruction of the associated musculature indicate that many aquatic early tetrapods fed by akinetic suction feeding, whereas others used crocodile-like jaw prehension. There is evidence that the earliest terrestrial tetrapods captured prey on land by jaw prehension rather than by tongue based feeding. Ontogenetic remodelling into a tongue supporting adult hyobranchium in early tetrapods can only be demonstrated in exceptional cases.

KURZFASSUNG

Diese Habilitationsschrift möchte zum besseren Verständnis der Physiologie und Lebensweise früher Tetrapoden des Paläozoikums und Mesozoikums beitragen. Sie basiert auf 13 eingefügte Arbeiten und konzentriert sich auf die Evolution osteologischer Korrelate, anhand derer Rückschlüsse auf die Struktur der Haut sowie die Art der Atmung und der Nahrungsaufnahme gezogen werden können. Der erste Teil der Habilitationsschrift besteht aus morphologischen und histologischen Untersuchungen der Hautknochen bei einer großen Auswahl von frühen Tetrapoden. Die äußere Skulptur der Hautknochen trug zur Konsolidierung der darüber liegenden Dermis (Lederhaut) bei; dies und die zahlreichen Hautverknöcherungen wie Osteoderme (Panzerplatten) und Dermalschuppen deuten darauf hin, dass Hautatmung im Gegensatz zu heutigen Lissamphibien keinen wesentlichen Teil des Gasaustausches ausmachen konnte. Es wird die Hypothese aufgestellt, dass eine weitere Funktion der Knochenskulptur in der Pufferung von CO_2-induzierter Azidose bestand, wenn sich die Tiere an Land aufhielten. Mehrere Gruppen früher Tetrapoden entwickelten unabhängig voneinander Osteoderme im Rumpf, die unter anderem die Wirbelsäule bei der Fortbewegung an Land unterstützen konnten oder bei wasserlebenden Formen den Auftrieb verringerten und als Kalzium-Reservoir dienten. Die Veränderungen in der Morphologie, Histologie und Anordnung der Dermalschuppen während des Fisch-Tetrapoden-Überganges erfolgte etwa simultan zur Entwicklung der Tetrapodenextremität und ermöglichte eine größere Flexibilität des Körpers und der Beine. Der zweite Teil der Habilitationsschrift beschäftigt sich mit dem Hyobranchial- oder Kiemenskelett früher Tetrapoden und seiner Rolle beim Atmen und Fressen. Das fischartige Kiemenskelett wurde bei einer unerwartet großen Anzahl früher Tetrapoden beibehalten. Dies zeigt, dass viele frühe Tetrapoden sowohl der Stamm- als auch der Kronengruppe als Adulte über innere Kiemen atmeten, während ihre Larven äußere Kiemen besaßen. Das Kiemenskelett und die Rekonstruktion assoziierter Muskeln zeigen, dass viele aquatische frühe Tetrapoden ihre Nahrung durch akinetisches Saugschnappen erbeuteten, während andere sie durch krokodilartiges Ergreifen mit den Kiefern fingen. Trotz spärlicher Fossilüberlieferung gibt es Hinweise darauf, dass die ersten an Land fressenden Tetrapoden noch keine bewegliche Zunge besaßen. Ein ontogenetischer Umbau des larvalen, kiementragenden Kiemenskelets in einen zungenstützenden Apparat kann bei frühen Tetrapoden nur in Ausnahmefällen belegt werden.

EXTENDED SUMMARY

1. Introduction

The evolution of tetrapods out of their fish-like ancestors in the Late Devonian and the subsequent conquest of land by limbed vertebrates is one of the major steps in vertebrate history. New discoveries have tremendously increased our knowledge of the structural and functional alterations involved (e.g., Coates & Clack 1991; Clack 1992, 2006, 2009; Ahlberg *et al.* 2005; Brazeau & Ahlberg 2006; Daeschler *et al.* 2006; Shubin *et al.* 2006; Niedźwiedzki *et al.* 2010; Pierce *et al.* 2013). However, studies of physiological aspects of early tetrapods are still in their infancy. This applies particularly to the skin structure, which determines major aspects in a vertebrate's metabolism, and the question of how early tetrapods were breathing and feeding. Research in this field relies almost entirely on the identification and interpretation of osteological correlates of soft-tissues because soft-part integument, muscles and respiratory organs like lungs and gills are hardly ever preserved in fossil vertebrates.

Early tetrapods evolved a variety of ossifications within their skin, comprising the dermal bones of skull and pectoral girdle as well as osteoderms (i.e. plate-like dermal armour) and dermal scales in the postcranial skeleton (Bystrow 1935, 1947; Dias & Richter 2003; Castanet *et al.* 2003). Dermal bones develop generally in the lower layer of the dermis and are usually penetrated by numerous canals that carried blood vessels and nerves (including the lateral line system of aquatic non-amniotes) to the external bone surface and into the directly overlying parts of the skin. For these reasons, the histomorphology of dermal bones as well as the structure of their external surface are well suited as osteological correlates of the soft-tissue integumentary structure in fossil vertebrates. In spite of this, the histology of dermal ossifications in early tetrapods has so far attracted only little attention in a limited number of taxa. Similar to the integumentary structure of early tetrapods, little is known about their hyobranchial apparatus (visceral or gill skeleton) that plays a fundamental role in breathing and feeding in fishes and tetrapods (e.g., Lauder & Reilly 1994; Deban & Wake 2000; Wake & Deban 2000). The investigation of how the hyobranchial apparatus of early tetrapods was altered in comparison to that of their fish-like relatives will thus give important insight in breathing and feeding of these extinct forms.

This habilitation thesis focuses on the integumentary structure and hyobranchial morphology of early tetrapods to contribute to the knowledge of the physiology and mode of life of early tetrapods. It consists of two main parts. The first part deals with dermal bones as osteological correlates of the skin structure and is again subdivided into sections on dermal bone sculpture and histology, osteoderms and dermal scales. The second part is concerned with the hyobranchial skeleton of early tetrapods and the implications for breathing and feeding.

The first tetrapods or limbed vertebrates are known from Late Devonian sediments, with the most famous taxa being *Acanthostega* and *Ichthyostega* from east Greenland (Clack 2012, and references therein). Tetrapodomorph fishes are the finned stem-tetrapods, with the paraphyletic, Middle to Late Devonian "elpistostegids" (*Panderichthys*, *Elpistostege* and *Tiktaalik*) comprising the closest known relatives of tetrapods (Schultze & Arsenault 1985; Vorobyeva & Schultze 1991; Shubin *et al*. 2006) (Fig. 1). Despite the evolution of limbs, the Late Devonian tetrapods appear to have been primarily aquatic animals, as indicated by the presence of fish-like internal gills; furthermore, the rather paddle-like, polydactylous limbs were inappropriate for carrying the body on land (Clack 2012). Therefore, the fish-to-tetrapod transition, which occurred in the Late Devonian, cannot be synonymised with the terrestrialisation of vertebrates. The first tetrapods that were capable of larger land excursions are known from the Early Carboniferous (Clack & Finney 2005; Smithson *et al.* 2012).

In the Extended Summary of this habilitation thesis, the phylogenetic results of Ruta & Coates (2007) and Schoch (2013) are taken as phylogenetic framework; for an alternative view of early tetrapod relationships, see Marjanović & Laurin (2013). The term "early tetrapod" is used for non-amniote limbed stem- and crown-group tetrapods of the Palaeozoic and Mesozoic. Apart from the Late Devonian forms, well-known limbed stem-tetrapods are the Carboniferous colosteids, adelogyrinids, and whatcheeriids (Fig. 1). Among early crown group tetrapods, two main lineages can be distinguished: (1) the temnospondyls (or amphibian-lineage) including extant lissamphibians (i.e. frogs, salamanders and caecilians), and (2) the amniote lineage comprising amniotes (mammals and reptiles including birds) and their stem-group. Temnospondyls were adapted to a large spectrum of habitats and are represented by aquatic, terrestrial and semi-terrestrial forms, spanning a wide size range from small, newt- or salamander-like forms like dissorophoids to the several-metre-long, crocodile-like stereospondylomorphs (i.e. stereospondyls and their stem-group). The amniote stem-group comprises the paraphyletic, Permo-Carboniferous "anthracosaurs" (including seymouriamorphs) and the Permo-Triassic chroniosuchians, both often resembling extant varanids or large salamanders in their habitus (Laurin 2000; Novikov & Shishkin 2000; Smithson 2000), and the lepospondyls, a diverse group of mostly small, newt- or lizard like forms (e.g., microsaurs) known from the Permo-Carboniferous (Schoch 2009).

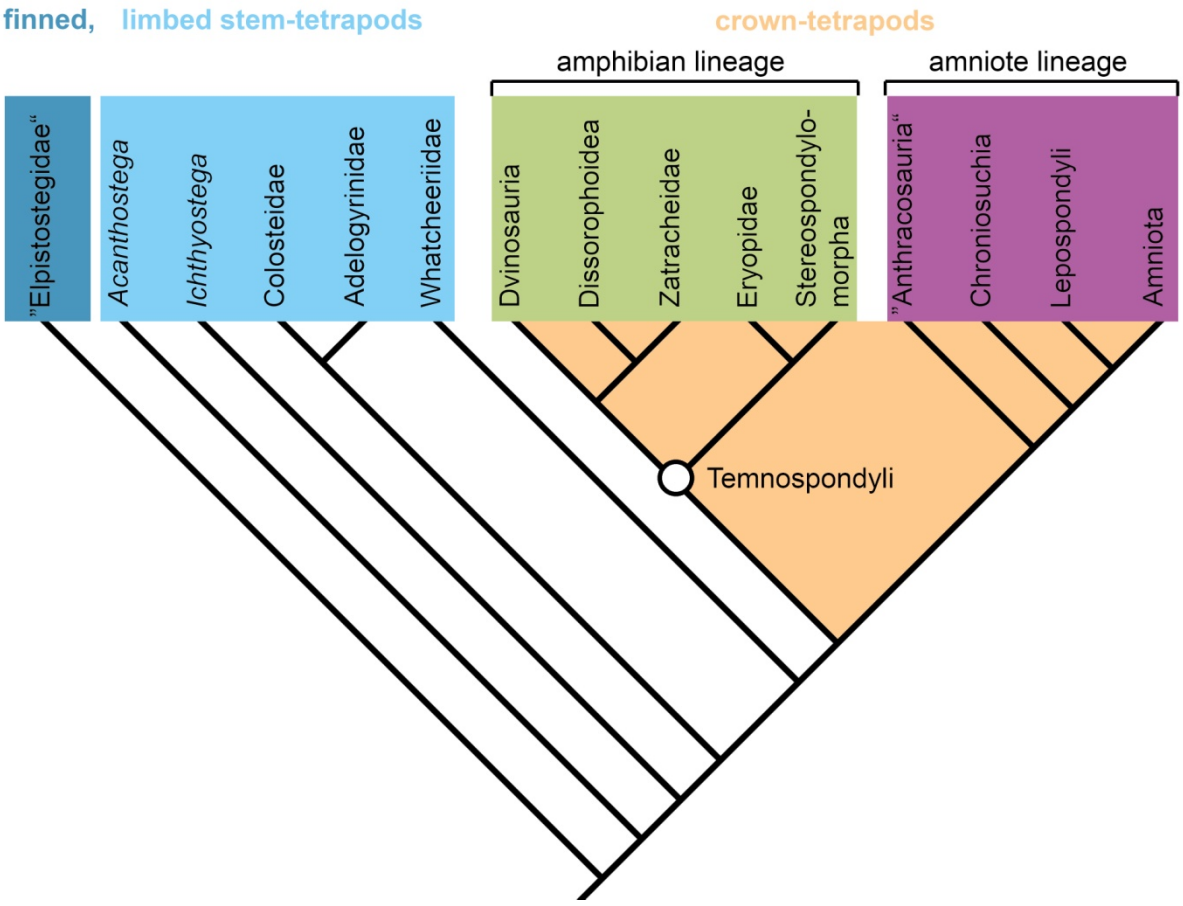

Figure 1: Interrelationships of early tetrapods. Topology of cladogram based on Ruta *et al.* (2007) and Schoch (2013).

2. Dermal ossifications and the integument in early tetrapods

2.1 Dermal bone sculpture in early tetrapods: external morphology, histology and possible functions

2.1.1 Introduction

The external or superficial surface of dermal bones of the skull, of the pectoral girdle and – if present – of osteoderms (see chapter 2.2) in early tetrapods are conspicuously sculptured (or ornamented) by tubercles, pits, ridges, and furrows on their external surface (Fig. 2A, B). The following chapter deals with the morphology and histology of dermal bone sculpture in a wide variety of early tetrapods. First, external sculptural patterns are distinguished, and the correlation between the position of the numerous openings of the vascular canals that penetrated the bone surface and the bone sculpture is studied (Witzmann *et al.* 2010 **[1]**).

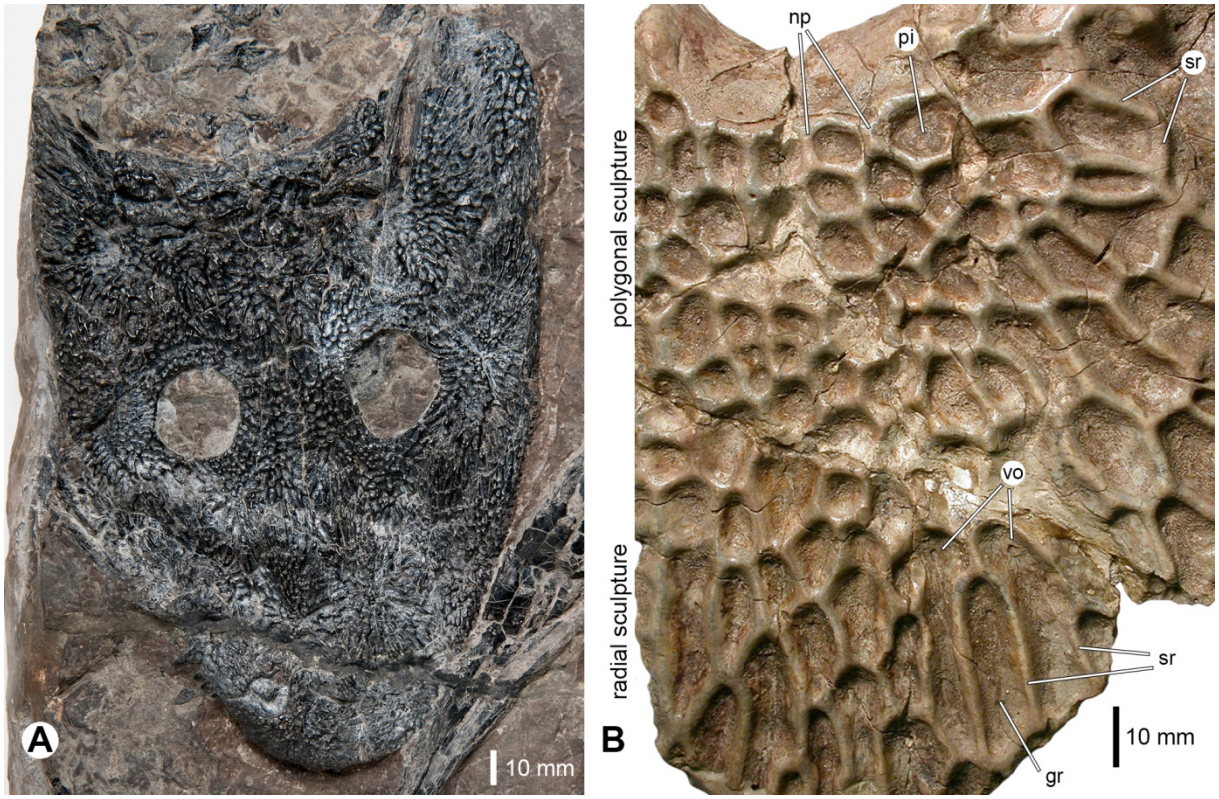

Figure 2: External morphology of dermal bone sculpture in early tetrapods, exemplified by stereospondylomorph temnospondyls. **A.** Skull roof of *Sclerocephalus bavaricus* from the Early Permian of Rhineland-Palatinate (MB.Am.442; photograph by Hwa Ja Götz, Museum für Naturkunde, Berlin); **B.** Squamosal bone of *Metoposaurus fraasi* (UCMP 27103, Arizona, USA), showing polygonal and radial sculpture. **Abbreviations: gr,** groove; **MB,** Museum für Naturkunde, Berlin; **np,** nodal point (sculpture); **pi,** pit; **sr,** sculptural ridge; **UCMP,** University of California Museum of Paleontology, Berkeley; **vo,** vascular opening.

Second, the phylogenetic signal of sculptural patterns is ascertained, and it will be investigated whether there is a correlation between the sculptural pattern and a presumed terrestrial or aquatic mode of life. Third, histological analyses of dermal bones of skull and pectoral girdle attach importance to the different types of bone tissues, the course of intrinsic bone fibres and the presence of extrinsic fibres; a further focus will be the degree of vascularisation and the type and morphology of the vascular canals, and the mode of growth of the dermal sculpture (Witzmann 2009 **[2]**). The results will be taken to draw conclusions about the integument in

which these bones were formed, and possible functional aspects of dermal bone sculpture in early tetrapods and during the fish-to-tetrapod transition will be discussed (Witzmann *et al.* 2010 **[1]**; Janis *et al.* 2012 **[3]**).

2.1.2 External patterns of dermal sculpture and their phylogenetic significance

In early tetrapods, two basic dermal sculptural patterns can be distinguished: the polygonal and the radial patterns, whereby transitions between the two different patterns exist (Fig. 2B). The tubercular sculpture is a special case and can be derived from these two patterns (see below). The polygonal sculpture consists of rounded or hexagonal cells, and each cell consists of a pit enclosed by sculptural ridges. Each pit contains at least one opening of a large vascular canal at its bottom. Because the points of intersection of sculptural ridges, the "nodal points", are visible in both basic sculptural patterns, they are interpreted here as homologous points that allow comparison between the different patterns. There is much variation between taxa concerning the height and width of the nodal points with respect to the sculptural ridges. Some early tetrapods possess a primarily radially arranged sculpture composed of sculptural ridges and furrows that radiate outwards from the ossification centre of each bone. This is basically a larval or juvenile character, but this pattern may also be retained in adult specimens. As Bystrow (1935) first demonstrated, the polygonal sculptural pattern develops ontogenetically from the radial pattern by the formation of dividing walls within the sculptural furrows. In certain taxa, the sculptural ridges are low or subdued, and the nodal points are well developed. Then, the sculptural pattern appears to be "tubercular".

Both polygonal and tubercular sculpture occurs in the earliest known tetrapods and their fish-like relatives (Witzmann *et al.* 2010 **[1]**; Witzmann 2010 **[4]**), so it cannot be ascertained which sculptural pattern is plesiomorphic for tetrapods. However, there seems to be a general trend in early tetrapod evolution that the sculptural morphology gets more regular and more pronounced from the stem group to more derived forms. The basic sculptural pattern of early tetrapods is retained in early amniotes (i.e. parareptiles and basal eureptiles). A principal component analysis (PCA) and a discriminant function analysis (DFA) of 47 taxa of early tetrapods using a set of 12 discrete characters of the external morphology of dermal sculpture were carried out (Witzmann *et al.* 2010 **[1]**). It shows that taxa that are interpreted as being largely aquatic have generally a more regular sculpture than presumably terrestrial ones. Furthermore, it demonstrates that dermal sculpture is well suited to distinguish some of the main temnospondyl lineages. However, when stem-amniotes and basal amniotes are included, it is apparent that the dermal sculptural pattern is of limited use to distinguish larger groups of tetrapods. Tests for phylogenetic significance were carried out for each of the 12 characters of dermal sculpture that were defined for the PCA using the software package Mesquite 2.6A. This test shows that the regularity of sculpture (constancy in width and height of ridges, and in width of nodal points, outline of polygons, presence or absence of pronounced tubercles) are phylogenetically significant.

2.1.3 Dermal sculpture and vascularisation

External morphology, thin sections and neutron scan imaging show that the pattern of the dermal sculpture reflects the course of the large vessels within the bone and within the dermis superficial to the bone surface (Witzmann *et al.* 2010 **[1]**). Within the dermal bone, the large blood vessels course roughly radially in the direction of the bone periphery, to be confluent with the vessels of neighbouring bones and to supply the growing bone at the periphery. The vessels that led to the superficial bone surface, and left the bone via the vascular openings, coursed within the dermis near the bone surface, and were always accompanied by sculptural

ridges and/or nodal points: either surrounded by a "funnel" in polygonal sculpture, or flanked within a furrow by ridges in radial sculpture towards the bone periphery. Ontogenetic data suggest that the vascular openings of the large canals induced the formation of sculptural ridges, either proximally, as an "axilla ridge", when the canals open obliquely to the surface, or around the opening, when the canals course approximately vertical to the bone surface. An increase in the number of vascular openings vertical to the bone surface within sculptural furrows accompanies the alteration of radial sculpture into the polygonal one. Bone and dermis were obviously so closely integrated with one another (and the dermis on top of the ridges and tubercles was so thin) that only the capillaries passed over the sculptural ridges and tubercles (as shown by imprints of vessels on the bone surface), and anastomosed with capillaries from the adjacent pit or groove along the ridges and tubercles. The association of the sculptural ridges (whatever the pattern) with the large blood vessels that left the superficial bone surface by vascular openings might suggest that the sculptural ridges and tubercles acted as a protection for these vessels against mechanical damage like abrasion or pressure from the outside, as the large vessels always lie *between* the sculptural elements. The coarser sculpture, with the more pronounced sculptural tubercles, in many rather terrestrial taxa might have provided enhanced resistance against mechanical damage of the vessels (and probably also of nerves and glands) on land.

2.1.4. Bone histology of dermal sculpture

Witzmann (2009 **[2]**) investigated histological thin sections prepared from dermal bones of skull and pectoral girdle of 18 taxa of early tetrapods, the "elpistostegid" *Panderichthys* and the porolepiform *Laccognathus*. Porolepiforms are Devonian sarcopterygians that are more closely related to lungfishes than to tetrapods (Janvier 1996). All dermal bones investigated here possess basically a microstructure that can be designated as a diploë structure, i.e., a cancellous (or trabecular) region is framed by an external and internal compact cortex of bone (Fig. 3A, B).In the thin sections, the sculptural tubercles and ridges on the external surface of the dermal bones are designated as "saddles" and the grooves or pits between them as "valleys". In *Laccognathus*, the sculptural tubercles are formed by tooth-like structures (dermal teeth or odontodes) consisting of dentine with a cap of enamel (Fig. 3A), whereas in early tetrapods and "elpistostegids", dermal sculpture consists solely of bone (Fig. 3B). Dental tissue on the outer surface of dermal bones (and dermal scales) is plesiomorphic for osteichthyans (see chapter 2.1.6). The thin sections reveal that the bony dermal sculpture in early tetrapods did not develop by local bone resorption as described for crocodile dermal bones that bear a superficially similar sculpture (de Buffrénil 1982; but see Vickaryous & Hall 2008), but rather by preferential growth of bone in tubercles and ridges (see also Bystrow 1935).

Sharpey's fibres. In *Laccognathus*, non-mineralised Sharpey's fibres penetrated the external bone surface between the odontodes (Fig. 3A). In early tetrapods and "elpistostegids", numerous fan-shaped, mineralised Sharpey's fibres are visible in the sculptural saddles, whereas they are often less abundant or absent in the sculptural valleys (Fig. 3B). In most early crown-group tetrapods, the Sharpey's fibres are distinctly larger in diameter than in *Laccognathus* and limbed and finned stem-tetrapods, and often more densely arranged. Sharpey's fibres represent extraneous, pre-existing fibres of the dermis that became progressively incorporated in bone during the centrifugal growth of the external cortex. Similar to Sharpey's fibres in mammals (Boyde 1972; Mowbray 2005) and the anchoring fibres in scales of certain teleosts (Sire 1985, 1986), the pre-existing, strong bundles of Sharpey's fibres in the dermis of early crown-group tetrapods might have induced the preferential growth of bone on the external surface, resulting in the dermal sculpture of tubercles and ridges that got more and more pronounced during ontogeny. The well mineralised fibres in early tetrapods

suggest a tight anchorage of the dermis to the external bone surface, especially to the ridges and tubercles, which served as the main points of

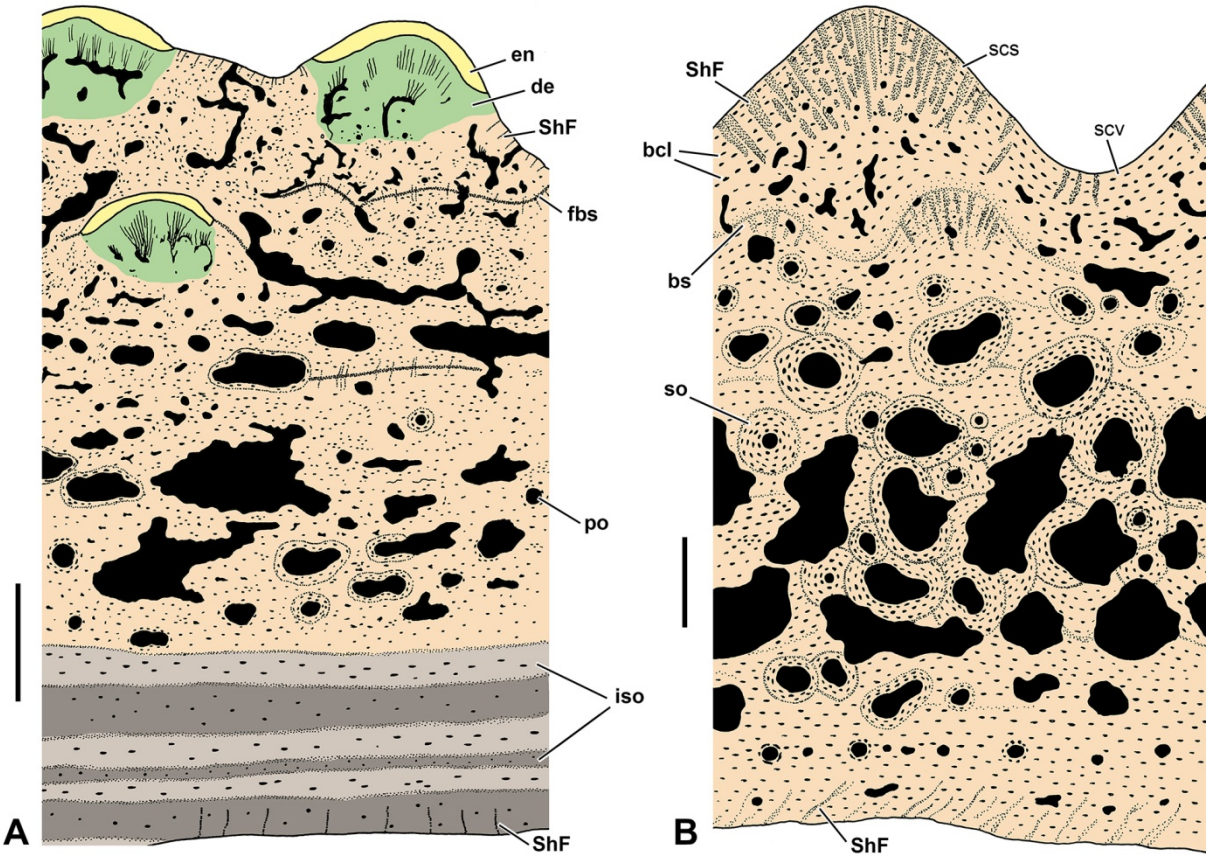

Figure 3: Schematic reconstructions of dermal bone histology in **(A)** an odontode-bearing sarcopterygian fish (*Laccognathus panderi*, Middle Devonian of Latvia, drawing based on MB.f. 17666), and **(B)** in an early crown-group tetrapod (based on several MCZ specimens of the eryopid temnospondyl *Eryops* from the Early Permian of Texas, USA). Scale bar equals 1 mm. **Abbreviations: bcl,** bone cell lacunae; **bs,** buried sculptural saddle of an earlier generation; **de,** dentine; **en,** enamel; **fbs,** former bone surface; **iso,** isopedine; **MB,** Museum für Naturkunde Berlin; **MCZ,** Museum of Comparative Zoology, Harvard, USA; **po,** primary osteon; **scs,** sculptural saddle; **scv,** sculptural valley; **ShF,** Sharpey's fibres; **so,** secondary osteon.

anchorage for the skin. Interestingly, a very similar pattern is visible in the shells of many turtles, in which dense connective tissue is tightly anchored to the sculptural projections of the dermal bones via Sharpey's fibres (e.g., Scheyer & Anquetin 2008). In the scales of many teleosts (Sire 1985, 1986) and osteoderms of lizards (Zylberberg & Castanet 1985; Levrat-Calviac & Zylberberg 1986), anchoring fibres extend uninterrupted from the ossified tissue into the dermis and continue until to the basement membrane of the epidermal-dermal boundary. Dense Sharpey's fibres that cross approximately perpendicularly the external cortex of osteoderms and interweave with the collagen fibres of the overlying dermis were also described by Hill (2006) in fossil and extant xenarthran mammals. It can be assumed that the Sharpey's fibres in dermal sculpture of early tetrapods likewise extended beyond the bone surface and were interwoven with the fibres of the dermis (and possibly extended until to the epidermal-dermal boundary, see chapter 2.1.6).

Bone tissue. The external cortices of the dermal bones consist mainly of parallel-fibred bone with growth marks, and the trabeculae of the cancellous middle region are composed mainly of parallel fibred bone that may be lined by lamellar bone of primary and secondary osteons. This middle region exhibits varying degrees of vascularisation, bone resorption and secondary bone

growth. The internal cortices of *Laccognathus* and the investigated finned and limbed stem-tetrapods consists of a plywood-like tissue (often called isopedine), that has been demonstrated so far only in fishes (Fig. 3A). In early crown-group tetrapods, isopedine in the internal cortex is reduced and replaced mostly by parallel fibred bone. In early crown-group tetrapods, transitions of parallel-fibred bone to "interwoven structural fibres" (ISF) *sensu* Scheyer & Sander (2004) may occur. This tissue consists of three dimensionally interwoven bundles of collagen fibres with a well ordered fibre bundle arrangement. Scheyer & Sander (2004) and Scheyer & Sánchez-Villagra (2007) interpreted ISF in the turtle shell and in dinosaur osteoderms as metaplastic in origin. Metaplastic bone develops via direct transformation of pre-existing, dense connective tissue, in absence of a periost, osteoblasts and osteoid (Haines & Mohuiddin 1968; Vickaryous & Hall 2008). Instead, fibroblasts take over the role of osteoblastic cells, but Scheyer *et al*. (2008) reported the involvement of "normal" osteoblasts in metaplastic development of the turtle shell. However, none of the dermal bones investigated are composed completely of ISF; this tissue is found often as islets or larger areas within parallel-fibred bone, and transitions can be observed in the same sections. As pointed out by Main *et al.* (2005), there exist many intermediate states between "normal" periosteal bone and the metaplastic bone (see also Goodwin & Horner 2004 and Scheyer & Sánchez-Villagra 2007).

2.1.5 Inferences of the histology of dermal bone sculpture for the soft-tissue integument

Development of bone via metaplasia requires a dense tissue such as articulation facets, attachment sites of tendons and ligaments, or a dense dermis (Haines & Mohuiddin 1968). Because metaplastic bone develops via direct transformation of pre-existing connective tissue (Haines & Mohuiddin 1968), its occurrence in dermal bones of several early crown-group tetrapods indicates that their dermis was rather dense and composed of an interwoven network of strong collagenous fibre bundles. The interpretation of a dense integument in early tetrapods is further supported by the mostly closely packed, thick bundles of Sharpey's fibres that extended from the bone surface into the dermis and certainly led to a strengthening and tight attachment of the dermis to the outer bone surface (see chapter 2.1.4). Consequently, one may suggest that many early crown-group tetrapods had a more consolidated integument compared to limbed and finned stem-tetrapods, in which ISF is absent and the Sharpey's fibres thinner and less densely arranged. Whereas most stem-tetrapods are regarded as water dwellers that hardly ever left the water, the earliest known temnospondyls of the Carboniferous are suggested to be capable of larger land excursions (Milner & Sequeira 1994; Holmes *et al.* 1998; Clack 2012). Therefore, a denser integument might have been required to reduce the extent of water loss in air and to withstand mechanical friction and abrasion during locomotion on land.

2.1.6 Changes of dermal bone structure during the fish-to-tetrapod transition

Bone structure. The dermal bones of limbed stem-tetrapods like *Acanthostega* or *Greererpeton* are more "fish-like" compared to those of the early crown-group tetrapods in the possession of isopedine in the internal cortex, the lack of ISF and in the thinner Sharpey's fibres within the external cortex. In turn, limbed stem-tetrapods are more "tetrapod-like" than their fish-like ancestors in that the dermal sculpture is more pronounced and forms a stronger relief. In early crown-group tetrapods, the sculpture is generally even more pronounced, what (in combination with the thicker and more densely arranged Sharpey's fibres) certainly led to an increased consolidation of the bone-dermis contact. The ability of the tetrapod dermis to form metaplastic ISF probably evolved somewhere below the split into the amphibian- (temnospondyl-) and

amniote lineage in a stem-tetrapod more crownwards than the colosteid *Greererpeton*. This is in accordance with the study of Sire & Huysseune (2003), who found a "normal" periosteal development without evidence of metaplasia in the postcranial armour plates of extant bony fishes. However, the only exception among non-tetrapod vertebrates might be the Silurian / Devonian galeaspid agnathans, in which Wang *et al.* 2005 reported a unique bony tissue called galeaspedin consisting of acellular laminar bone. This tissue was interpreted by Sire *et al.* (2009) as probably metaplastic in origin.

Odontodes versus bone sculpture. As mentioned above, the presence of dental tissue (dentine and enamel or enameloid) on the external surface of dermal bones as either tubercles or ridges (odontodes) can be regarded as plesiomorphic for osteichthyans and even for vertebrates in general (Janvier 1996). In early tetrapods and their immediate stem-forms, all dental tissue was lost in the exoskeleton, and the tubercles and ridges on the dermal bone surface consist completely of bone. The pattern of superpositional growth and arrangement of odontodes (Sire *et al.* 2009, and references therein) closely resembles that of bony sculptural tubercles or ridges of early tetrapods (Fig. 3), suggesting that the bony sculpture took over parts of the functional role of the odontodes. By the interaction of epidermal and ectomesenchymal tissue in the production of the odontodes, and their development above (enamel) and below (dentine and bone) the epidermal-dermal junction (Ørvig 1968), the outer skeletal surface was well integrated with both dermis and epidermis via the odontodes. Because of the superficial position of the odontodes within the skin, they may have stabilised the integument and served for mechanical protection of the soft-tissue in the "valleys" between them. The epidermal (and superficial dermal) portion of the exoskeleton was lost when the dental components were reduced. The bony sculpture laid deeper in the integument than the odontodes and did not reach the epidermis, as shown by the Sharpey's fibres that penetrate the surface of the sculptural elements. As outlined above, it is interpreted here that the bundles of Sharpey's fibres, that are found mainly and most closely packed in the bony tubercles and ridges, still maintained an association between the outer bone surface and the superficial parts of the dermis and epidermal-dermal junction, respectively, and led to a strengthening of the integument and its tight connection to the bone surface. Like the odontodes, the bony ridges and tubercles certainly also protected the numerous blood vessels mechanically that coursed in furrows or pits between them (see chapter 2.1.3). The difference, however, is that the bony tubercles and ridges were embedded deeper within the dermis and did not extend to or beyond the epidermis. This might be the reason why the skin was more tightly bound to the bone surface by Sharpey's fibres after the odontodes were reduced; this difference is well visible between the odontode-bearing *Laccognathus* with loosely arranged, non-mineralised Sharpey's fibres and *Panderichthys*, that has a bony sculpture and stronger, mineralised Sharpey's fibres.

2.1.7 Dermal sculpture and cutaneous respiration

Bystrow (1947) assumed that vascularisation of dermal sculpture in early tetrapods was associated with cutaneous respiration. He based his assumption not on the large vessels that opened within the sculptural cells and furrows, but explicitly on a capillary network ("rete vasculosum") *within* the external cortex. However, thin sections show that the superficial portion of the external cortex is often poorly vascularised or is even avascular, which renders a connection between cutaneous respiration and the capillaries doubtful (Witzmann 2009 **[2]**). The capillaries in the deeper parts of the external cortex rather indicate that bone growth was faster in an earlier ontogenetic phase and slowed down later in ontogeny. However, regarding the large number of vascular openings on the bone surface and the associated large vessels, and their ramification into small capillaries on the bone *surface* (see chapter 2.1.3), a respiratory function cannot be ruled out completely. Nevertheless, many early tetrapods were

comparatively large with an unfavourable ratio of surface area to body volume and often possessed well-ossified, tightly set ossified scales (see chapter 2.3). Furthermore, the presumed dense skin as indicated by the presence of metaplastic interwoven structural fibres (ISF) and numerous mineralised, strong Sharpey's fibres in the dermal bones argues against a large-scale gas exchange function as seen in lissamphibians. Apart from this, there is evidence that the epidermis in early tetrapods was rather similar to amniotes in being more strongly cornified and more complex, compared with lissamphibians (Maddin *et al.* 2007).

2.1.8 Sculptured dermal bones as adaptation for terrestrial acidosis?

Dermal bone sculpture in early tetrapods probably did not serve a single function, and it must be considered that a character can be involved in new functional aspects. Apart from stabilising the integument as outlined above, dermal bone sculpture may have taken over a significant role in CO_2 metabolism in early tetrapods. These animals probably would have lacked adequate means for CO_2 elimination, such as the capacity to achieve the high ventilation rates made possible by costal aspiration as in amniotes, the ability to lose significant amounts of CO_2 via the skin (as e.g. in lissamphibians), or the kidney function necessary to increase blood HCO_3^- concentrations to levels required to fully compensate for respiratory acidosis. Janis *et al.* (2012 **[3]**) proposed that a key function of the dermal bone sculpture (associated with strong vascularisation that is characteristic of early tetrapods, see chapter 2.1.3) was to buffer CO_2-induced acidosis and perhaps also lactic acidosis induced by periods of anaerobic activity. This would have allowed these animals to maintain homeostasis for longer periods of time during land excursions. The longer an individual could survive in this new environment, the more it would be able to exploit terrestrial resources. This hypothesis is supported by studies on living tetrapods showing that dermal bone has the physiological capacity to buffer acidosis caused by the build-up of CO_2 and lactic acid (e.g., Warren & Jackson 2005). Comparison of dermal sculpture between different groups of early tetrapods has shown that dermal sculpture is indeed coarser with pronounced tubercles and ridges in terrestrial early tetrapods than in more aquatic ones (see chapter 2.1.2). Dermal sculpture is reduced or lost only in those forms that would have been small enough to have been lissamphibian-like bimodal breathers, losing CO_2 through their skin (with reduced scales), or in stem-amniotes (like "anthracosaurs") with evidence of costal ventilation. However, the picture is not always consistent: while the majority of aquatic taxa had less pronounced sculptured dermal bone, a few showed more pronounced sculpturing (e.g., plagiosaurid stereospondyls or colosteids like *Greererpeton*). These forms were predominantly bottom-dwelling taxa, with heavily ossified skeletons, and dermal sculpture may have added to this ballast weight. Alternatively, these aquatic forms may have specialised for hypercapnic or hypoxic aquatic environments, as indicated by their flattened body forms, and their integumental features represented an adaptation for carbonic and metabolic acid buffering in this type of environment (see also Ultsch 2012). The hypothesis of Janis *et al.* (2012 **[3]**) that sculptured dermal bones are a response to terrestrial hypercapnia, and that they had the function of buffering acidosis, is speculative in its approach: at present it is impossible to confirm or refute this hypothesis with histological studies of fossil vertebrates. However, the hypothesis is strongly supported by the observed dermal morphology in the diversity of early tetrapods in correspondence with their presumed ecologies (terrestrial or aquatic), as determined by other anatomical features.

2.2 Osteoderms (dermal armour plates) in early tetrapods

2.2.1 Introduction

Additional to dermal scales (see chapter 2.3), different lineages of early tetrapods have evolved dermal armour consisting of plate-like, often sculptured osteoderms in the postcranial skeleton that vary conspicuously in size, shape, and mode of articulation (e.g., Panchen 1959; DeMar 1966, 1968; Golubev 1998; Novikov *et al.* 2000; Hellrung 2003; Dilkes and Brown 2007; Dilkes 2009; Witzmann *et al*. 2008 **[5]**). This chapter is concerned with the structure of early tetrapod osteoderms that has been investigated by Witzmann & Soler-Gijón (2010 **[6]**) and Buchwitz *et al.* (2012 **[7]**). These authors selected osteoderms of certain temnospondyls (the plagiosaurid stereospondyls *Plagiosuchus* and *Gerrothorax*, the possible plagiosaurid *Peltobatrachus*, and the dissorophoids *Aspidosaurus*, *Platyhystrix* and *Cacops*) and of different chroniosuchians. Chroniosuchians are Permo-Triassic stem-amniotes (Figs 1, 4) that are subdivided into two main subgroups, bystrowianids and chroniosuchids. Whereas Witzmann & Soler-Gijón (2010 **[6]**) investigated the osteoderm structure of the bystrowianid *Bystrowiella*, Buchwitz *et al.* (2012 **[7]**) studied the osteoderms of four chroniosuchid taxa (*Chroniosuchus*, *Chroniosaurus*, cf. *Uralerpeton*, and *Madygenerpeton*). Chroniosuchians are regarded as terrestrial or semi-terrestrial early tetrapods (Laurin *et al*. 2004), and the elaborate mechanism of articulation between the osteoderms (Novikov *et al*. 2000; Witzmann *et al*. 2008 **[5])** may have stabilised the vertebral column (Clack & Klembara 2009; Buchwitz & Voigt 2010). It will be discussed which inferences can be drawn from the bone microstructure and histology of osteoderms concerning functional aspects, the associated soft parts and the phylogenetic significance.

Figure 4: The chroniosuchian *Chroniosaurus dongusensis* (PIN 3585/124) from the Late Permian of the Orenburg Province, Russia, showing the skull and the anterior trunk with a row of osteoderms covering the vertebral column. **Abbreviations: ost,** osteoderms; **PIN,** Paleontological Institute and Museum of the Russian Academy of Sciences, Moscow, Russia.

2.2.2 Osteoderm microstructure and functional considerations

Osteoderms are plate-like dermal bones showing a diploë structure in thin sections corresponding to the dermal bones of the skull and pectoral girdle (see chapter 2.1.4). Comparison of bone microstructure revealed that the studied osteoderms show a wide range of compactness values that may reflect different lifestyles (Witzmann & Soler-Gijón 2010 **[6]**; Buchwitz *et al.* 2012 **[7]**). Among temnospondyls, the stereospondyls *Peltobatrachus* and

Gerrothorax have an extensive external compact cortex that accounts for more than half the thickness of the bone. The most compact bone structure is shown by *Plagiosuchus*, whose middle region is compact rather than cancellous and therefore, no true diploë structure is present. In contrast, the osteoderms of the investigated dissorophids are very lightly built with extensive vascular spaces, gracile trabeculae and thin cortices. At least in *Aspidosaurus* and *Platyhystrix*, the cortex is composed of a plywood-like tissue. This osteoderm structure provides maximum stability and minimum bone mass, and is consistent with the interpretation that the osteoderms of dissorophids served to strengthen the vertebral column during terrestrial locomotion (Dilkes & Brown 2007; Dilkes 2009).

The much more massive osteoderms that covered the complete body of *Gerrothorax* and the back of *Plagiosuchus* might be interpreted as serving for reduction of buoyancy in these aquatic animals. Especially *Gerrothorax* can be regarded as a bottom-dwelling, lurking predator (Hellrung 2003; Witzmann & Schoch 2013 **[12]**) that shows pachyostosis of the ribs (Castanet *et al*. 2003) and a well ossified endocranium (Witzmann *et al.* 2012) that increased its body weight. Furthermore, the extensive dermal armour of *Gerrothorax* constituted a calcium reservoir, as indicated by the cyclical resorption events preserved in the external cortex (Witzmann & Soler-Gijón 2010 **[6]**). These structures can be interpreted as a physiological response to periodic changes in salinity of the aquatic environment. When the degree of salinity decreased or the animal encountered freshwater, it may have undergone physiological stress, and calcium has been remobilised from the osteoderms. Sedimentological studies support this interpretation and indicate that *Gerrothorax* lived in a large, brackish influenced delta (Schoch & Wild 1999; Hellrung 2003). These periodic changes in salinity might be explained in two ways: either *Gerrothorax* migrated periodically from brackish to freshwater, e.g. for spawning; or *Gerrothorax* remained rather territorial and the salinity changed periodically by input of freshwater from the hinterland, e.g. during the rainy season. In *Peltobatrachus*, whose postcranial morphology suggests a primarily terrestrial mode of life (Panchen 1959) the osteoderms are similarly massive as in *Gerrothorax* and probably served mainly for protection.

Among chroniosuchians, quantitative osteoderm bone compactness analyses reveal high overall bone compactness in the bystrowianid *Bystrowiella* that resembles that of the investigated aquatic plagiosaurids (Buchwitz *et al.* 2012 **[7]**). In *Chroniosaurus* and *Madygenerpeton*, osteoderm bone structure is slightly less compact, whereas *Chroniosuchus* and cf. *Uralerpeton* have a comparatively thick trabecular middle region and low compactness values similar to the terrestrial dissorophids. These highly variable compactness profiles of chroniosuchian osteoderms might indicate an ecological differentiation of chroniosuchians within the aquatic-terrestrial spectrum (Buchwitz *et al.* 2012 **[7]**).

2.2.3 Dermal sculpture of osteoderms and extraneous and intrinsic fibres

The external surface of most osteoderms in early tetrapods bears dermal sculpture corresponding to dermal bones of skull and pectoral girdle (see chapter 2.1), that may be polygonal (reticulate) or tubercular (Witzmann *et al*. 2008 **[5]**; Witzmann & Soler-Gijón 2010 **[6]**; Buchwitz *et al.* 2012 **[7]**). Also the bone histology of dermal sculpture with the associated mineralised Sharpey's fibres corresponds to the pattern described in chapter 2.1. The internal cortex of *Gerrothorax* osteoderms is penetrated by strong bundles of long Sharpey's fibres that presumably connected the osteoderms to the underlying tendons and muscles of the trunk. The Sharpey's fibres converge towards the centre of the osteoderm, and a corresponding pattern and attachment of the osteoderms to the trunk is visible in *Peltobatrachus*. In contrast, similarly strong, anchoring fibres are absent in the internal cortex of *Bystrowiella* and in dissorophids, since these taxa have osteoderms that are tightly attached to the neural spines by

co-ossification (Witzmann *et al*. 2008 **[5]**; Witzmann & Soler-Gijón 2010 **[6]**). Buchwitz *et al.* (2012 **[7]**) found sets of antero- and posteroventrally directed Sharpey's fibres in the non-overlapping medial part of the internal cortex of the investigated chroniosuchid osteoderms. These fibres indicate the insertion of epaxial muscle systems to the ventral side of the osteoderms. The muscle connection of the osteoderms in chroniosuchids can be interpreted as part of a trunk-carrying construction that resembles the trunk-bracing systems of crocodylians (e.g., Salisbury & Frey 2000; Schwarz-Wings *et al.* 2009). This finding supports the hypothesis that the chroniosuchian osteoderm series evolved in a terrestrial context and primarily served as a device that supported terrestrial locomotion. However, the highly variable compactness profiles of chroniosuchian osteoderms as outlined above are in conflict with the interpretation of a primarily terrestrial lifestyle.

Plagiosuchus has osteoderms that were not co-ossified with endoskeletal elements like vertebrae or ribs. They bear no dermal sculpture comparable to dermal bones of other early tetrapods but rather a roughened external surface. The Sharpey's fibres are extensively developed and equally distributed in the external and internal regions and directed to the proximal portion of the osteoderm. The extensively developed Sharpey's fibres in *Plagiosuchus* suggest a tight anchorage of the osteoderm within the dermis. As in dermal bones of skull and pectoral girdle, three-dimensionally interwoven structural fibres (ISF) are identified in osteoderms of *Chroniosaurus* (Buchwitz *et al.* 2012 **[7]**), *Bystrowiella*, *Plagiosuchus* (Witzmann & Soler-Gijón 2010 **[6]**), and, to a lesser degree, in osteoderms of *Gerrothorax* (Witzmann 2011 **[9]**) and co-occurs with parallel-fibred bone.

2.2.4 Phylogenetic considerations

Recent phylogenetic analyses of early tetrapods suggest that the osteoderms in dissorophids, plagiosaurids, and chroniosuchians evolved independently (Yates & Warren 2000; Ruta *et al*. 2007; Schoch 2013). This is also indicated by the unique structure of the dissorophid osteoderms investigated by Witzmann & Soler-Gijón (2010 **[6]**) that might be a synapomorphy of the group. The osteoderms of *Gerrothorax* and *Peltobatrachus* resemble each other in the extensively thick external cortex and the strong Sharpey's fibre bundles penetrating the thinner internal cortex. Furthermore, both taxa have a tubercular dermal sculpture. However, these similarities do not necessarily support the proposed close relationship of *Peltobatrachus* and plagiosaurids (Panchen 1959; Milner 1990) but can be explained with functional reasons: the thick cortex might have served for protection, and the large bundles of Sharpey's fibres in the internal cortex anchored the osteoderms to the subdermal connective tissue, since no co-ossification with vertebrae is present. Furthermore, tubercular sculpture on osteoderms is not restricted to these taxa but occurs also in certain chroniosuchians (Buchwitz *et al.* 2012 **[7]**), and can easily be derived from polygonal sculpture (see chapter 2.1.2). In contrast, the described differences in histological structure of the osteoderms in *Gerrothorax* and *Plagiosuchus* clearly suggest an iterative evolution of osteoderms within plagiosaurid stereospondyls.

The independent acquisition of osteoderms in different lineages of early tetrapods reflects the potential of the dermis in tetrapods to develop skeletal structures. Additional to the dermal scales in early tetrapods that probably represent a heritage from nontetrapod ancestors (see chapter 2.3) and the large plate-like osteoderms of armoured temnospondyls and chroniosuchians described in this study, small, irregular osteoderms have been reported among early tetrapods locally in the trunk or gular region (Witzmann & Soler-Gijón 2010 **[6]**, and references therein). The skeletogenic potential of the tetrapod dermis is also shown by extant anurans in which osteoderms evolved independently within different lineages (Ruibal & Shoemaker 1984; Quinzio & Fabrezi 2012), as well as in several groups of amniotes (e.g.,

Scheyer & Sander 2004; Hill 2005, 2006; Vickaryous & Hall 2006, 2008). According to Main *et al.* (2005) and Vickaryous & Hall (2008), deep homology exists between osteoderms in the different tetrapod lineages because they have a common origin in the skeletogenic potential of the dermis. The advantages of osteoderms are manifold (like support of the vertebral column, the reduction of buoyancy, physiological calcium reservoir, or simply protection against predators). The presence of ISF in osteoderms of the quite distantly related chroniosuchians (amniote lineage) and the plagiosaurid stereospondyls (amphibian lineage) supports the above stated assumption (chapter 2.1.6) that the potential for metaplastic ossification in the dermis was present very early in tetrapod evolution.

2.3. Structure of dermal scales in early tetrapods and their fish-like relatives

2.3.1 Introduction

Most early tetrapods were covered by ossified dermal scales from which two different types can normally be distinguished (Romer 1972; Boy 1988; Witzmann 2007 **[8]**, 2011 **[9]**): rhombic or spindle-shaped "gastral scales" that form rows arranged in a chevron pattern on the ventral face of the trunk between pectoral and pelvic girdle, and thin "round-oval" or "dorsal scales" covering the dorsal portion of the trunk together with flanks, tail and limbs (Fig. 5).

Schultze (1977) reconstructed the hypothetical ancestral scale of stem-osteichthyans as being thick and rhombic in outline, with tubercles of dentine covering a cancellous layer of bone, which is followed internally by a basal layer of plywood-like tissue (i.e. isopedine). These scales were arranged in oblique rows on the body in basal osteichthyans, and each scale was overlapped by adjoining scales anteriorly and dorsally on the external surface and ventral to a distinct keel on the internal side (Schultze 1977). The scales of "elpistostegids" are derived in the absence of dental tissue and the presence of dermal sculpture that is composed solely of bone, but are plesiomorphic in their rhombic outline and arrangement in oblique rows (Gross 1930; Schultze & Arsenault 1985; Daeschler *et al.* 2006). "Elpistostegids" have anteromedially directed rows of rhombic scales both on the ventral and the dorsal face of the body (Witzmann 2011 **[9]**). This chapter intends to show which alterations occurred in morphology, histology and arrangement of ossified dermal scales during the fish-to-tetrapod transition, and interprets how and why these changes occurred.

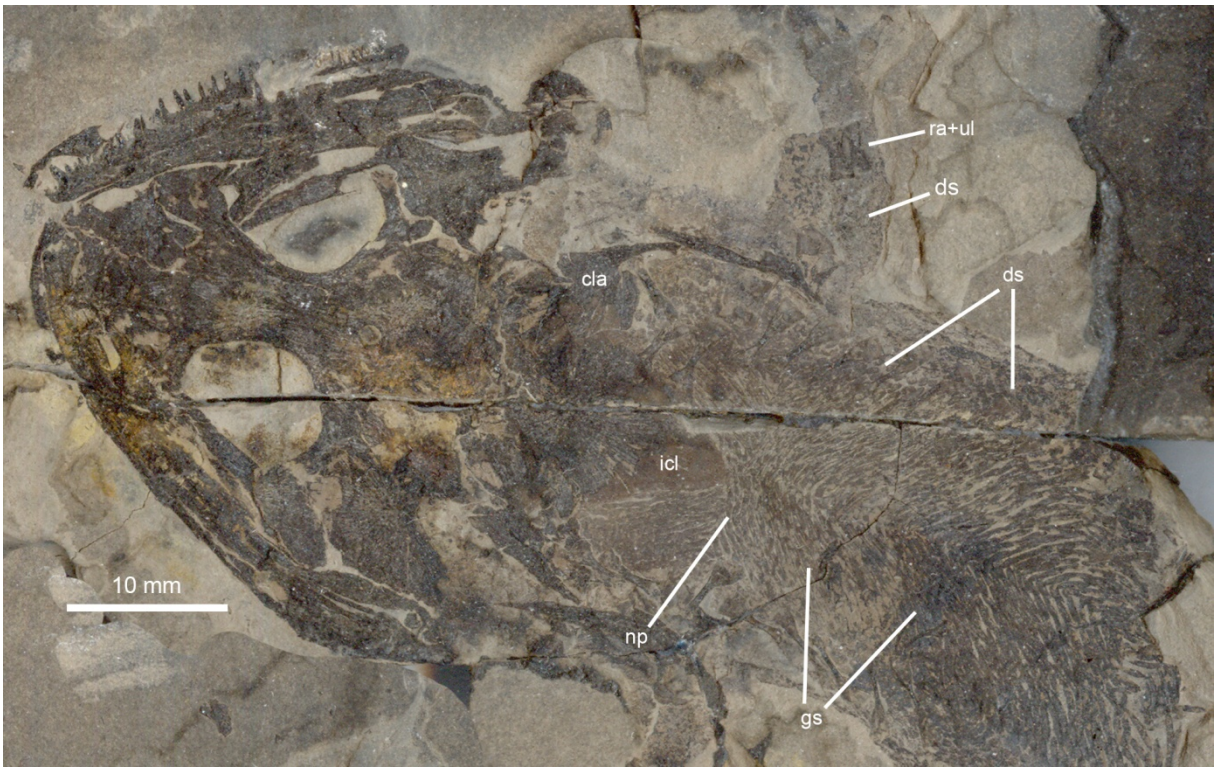

Figure 5: Juvenile specimen of the stereospondylomorph temnospondyl *Sclerocephalus haeuseri* from the Early Permian of Rhineland-Palatinate (MB.Am.1203), showing spindle-shaped gastral and round ovate dorsal scales. **Abbreviations: cla,** clavicula; **ds,** dorsal scales; **gs,** gastral scales; **icl,** interclavicula; **MB,** Museum für Naturkunde Berlin; **np,** nodal point (scales); **ra,** radius; **ul,** ulna.

2.3.2 Ventral or gastral scales

Arrangement of ventral or gastral scales. The gastral scales of early tetrapods are derived from the ventral scales of "elpistostegids". Although the gastral scales of early tetrapods show an arrangement that corresponds to the oblique ventral scale rows of "elpistostegids", they meet in the ventral midline in a different manner. "Elpistostegids" possess a single median row of hexagonal scales on the ventral side of the trunk that articulate with the medialmost scales of each oblique scale row. This median row is absent in early tetrapods; instead, the medialmost gastral scales from opposite sides show alternating overlap. Characteristic for most early tetrapods is the "nodal point" (Fig. 5) posterior to the interclavicle, in which the anteriorly and posteriorly directed chevrons of gastral scales meet (Witzmann 2007 **[8]**). In "elpistostegids", all ventral oblique rows of scales are posterolaterally directed and no "nodal point" is developed.

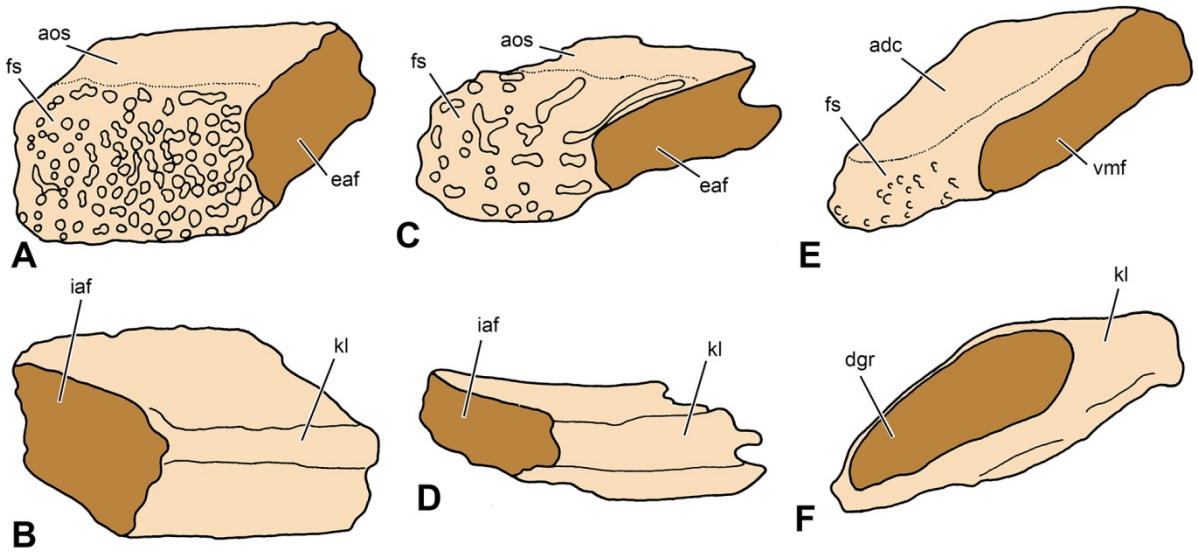

Figure 6: Comparison of ventral scales of the "elpistostegids" *Panderichthys* **(A, B)** and *Elpistostege* **(C, D)** with rhombic gastral scales of the colosteid *Greererpeton*. Schematic drawings, not to scale. For each scale, the external view is shown at the top, and the internal view is shown at the bottom. *Panderichthys* and *Greererpeton* redrawn after Witzmann (2011 **[9]**) and *Elpistostege* redrawn after Schultze & Arsenault (1985). **Abbreviations: adc,** anterodorsal crest; **aos,** anterior overlap surface; **dgr,** dorsal groove; **eaf,** external articulation facet; **fs,** free surface; **iaf,** internal articulation facet; **kl,** keel; **vmf,** ventromedial facet.

Origin of the rhombic gastral scale. To understand how scale morphology was altered during the fish-to-tetrapod transition, it is necessary to identify homologies in the rhombic scales of "elpistostegids" and the gastral scales of early tetrapods (Fig. 6). Homologous "landmarks" in the "elpistostegid" scale are (1) the keel on the internal surface, which serves as anchoring point for Sharpey's fibres to connect the different oblique rows of scales in osteichthyans (Schultze 1966; Gemballa & Bartsch 2002; Witzmann 2011 **[9]**), and which frames the internal articulation facet of the scale; and (2) the external and internal articulation facets and the (sculptured) free external surface (Fig. 6). The morphological transformation between the "elpistostegid" scale and the gastral scale of early tetrapods can be reconstructed as follows. The internal articulation facet became proportionally distinctly longer, measuring more than half the length of the scale (Fig. 6B, D, F). The keel became correspondingly shorter, but increased in width and occupied the width of the medial portion of the scale. It still frames the internal articulation facet (or dorsal groove), but over a longer distance than in the "elpistostegid" scale. Posteriorly, the frame is formed by a thickened, posterior bulge-like crest, and anteriorly by a more slender, anterodorsal crest. In this way, the internal facet became conspicuously deeper in early tetrapods and can now be designated as "dorsal groove". The area on the external surface that was overlapped by the anterior scale row proportionally increased in size. Accordingly, the free surface of the scale became narrowed. The external facet of articulation attained an elaborate, concavo-convex surface. These morphological alterations caused (1) a tighter connection between the gastral scales *within* a scale row, and (2) increased anteroposterior overlap *between* the scale rows.

Scale ontogeny: rounded and spindle-shaped gastral scales. Thin, ovoid gastral scales were described in early growth stages of early tetrapods and designated as "larval", and their transition to the spindle-shaped morphology can be demonstrated in further ontogeny (Witzmann 2007 **[8]**) (Fig. 7). The presence of ovoid gastral scales in adult specimens, e.g. in the Devonian tetrapod *Tulerpeton*, can thus be interpreted as a retained "larval" morphology. Spindle-shaped gastral scales and rhombic gastral scales can be traced back to basically the same morphology. Compared to the rhombic scale, the spindle-shaped scale is proportionally

elongate and slender, with a more tapering medial end. Due to the small size of the anterior crest, there is no (or little) overlap between the rows of spindle-shaped scales. As described by Witzmann (2007 **[8]**), the spindle-shaped gastral scales are the ontogenetic precursor of the rhombic gastral scales (Fig. 7). The rhombic outline is attained by the expansion of the slender crest that borders the dorsal groove anteriorly, and by a thickening of the posterior bulge-like crest. The largely smooth dorsal groove of the spindle-shaped gastral scales becomes the well-defined facet or groove of the rhombic gastral scale.

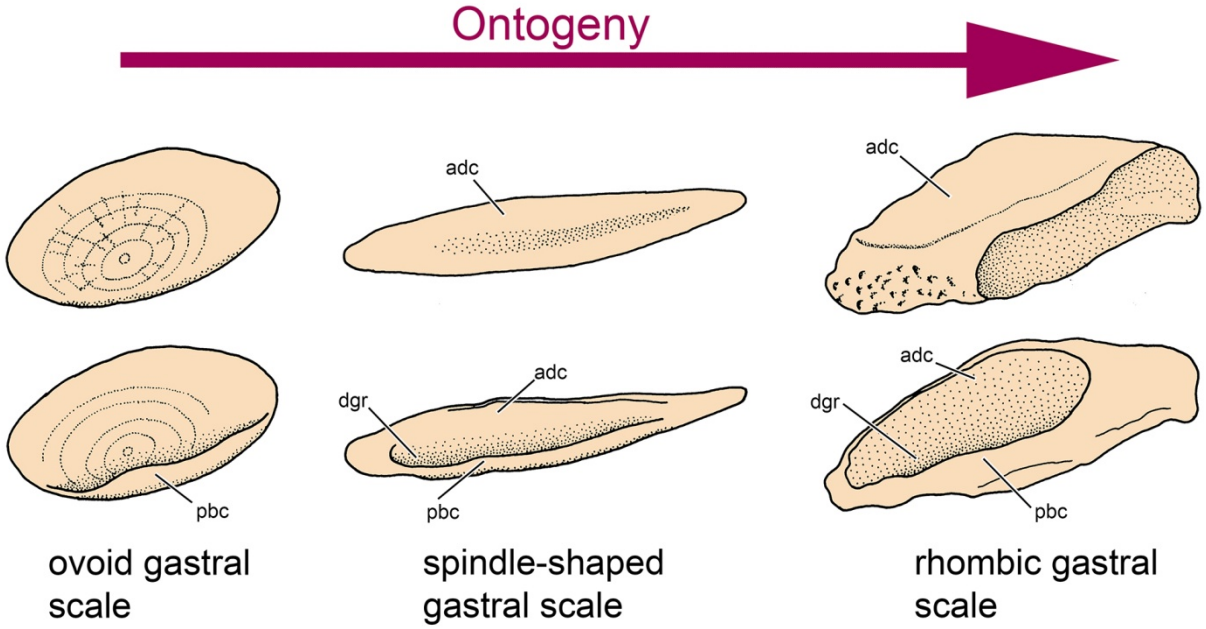

Figure 7: Comparison of ovoid, spindle-shaped and rhombic gastral scales in external view (top) and internal view (bottom). Schematic drawings, not to scale. After Witzmann (2011 **[9]**). **Abbreviations: adc,** anterodorsal crest; **dgr,** dorsal groove; **pbc,** posterior bulge-like crest.

2.3.3 Dorsal or round-oval scales

It is more parsimonious to assume that the dorsal round-oval scales of early tetrapods were derived from the rhombic "elpistostegid"-type of scale rather than being *de novo* structures, and convergent examples of a transformation from rhombic to rounded scales can be seen in the evolution of actinopterygians and different lineages of fish-like sarcopterygians (e.g., Gross 1966; Schultze 1966, 1977; Janvier 1996; Sire *et al*. 2009). This transformation during the fish-to-tetrapod transition can be reconstructed as follows. In the "larval" ovoid scale, proportional elongation of the scale ceased early in ontogeny, and so did the development of the posterior crest. Further growth of the scale was more compensational, resulting in a rounded shape. This evolutionary scenario is reflected in the gastral scalation in the ventrolateral part of the trunk in early tetrapods, where an almost continuous transition from gastral scale to round dorsal scale morphology is visible. As gastral and dorsal scales develop from the same *anlagen*, round-oval "dorsal" scales can also be observed to cover the ventral face of the trunk in certain early tetrapods (Witzmann 2007 **[8]**, and references therein), representing a paedomorphic trait. Conversely, the colosteid *Colosteus* has rhombic scales not only on the ventral, but also on the dorsal side of the trunk, showing that the dorsal scale *anlagen* still had the ability to attain the plesiomorphic rhombic scale morphology.

2.3.4 Evolutionary and functional implications

Apparently at roughly the same time when digits appeared, the rhombic scales of "elpistostegids" were altered and differentiated into ventral gastral and dorsal round-oval scales, thus being one of the most rapid morphological changes during the fish-to-tetrapod transition. Once established in tetrapods, especially the gastral scales were retained as a conservative character in different lineages of early tetrapods, in both the amphibian and the amniote lineage. The transformation of the scalation pattern might have been connected with the need for a more flexible trunk during terrestrial or semiterrestrial locomotion, and a reduction of weight. The following characters indicate that the gastral and dorsal scalation in early tetrapods was more flexible and probably allowed a larger degree of trunk flexion of the trunk compared to "elpistostegids": (a) the contralateral rows of gastral scales articulate in an alternating, overlapping fashion; (b) the mode of overlap of the spindle shaped ("juvenile") gastral scales allowed telescoping of the scales within the rows during sideward flexion of the body; (c) though the rhombic ("adult") gastral scales were more tightly connected *within* the rows, the anterior overlap surface became proportionally larger than in "elpistostegids", allowing more overlap *between* scale rows; (d) dorsal scales were thinner and certainly more flexible than ancestral rhombic scales. Also the "nodal point" contributed to an enhanced flexibility of the anterior trunk region and forelimbs: when head plus girdle moved to one lateral side, the degree of overlap between the anterolaterally directed rows of this side increased, whereas the degree of overlap between rows of the other side decreased. As the forelimbs are located lateral to the nodal point in the "gap" between anterolaterally and posterolaterally directed rows (Fig. 5), the forelimbs had a greater degree of freedom.
Scale histology in early tetrapods is simplified compared to their finned ancestors, resulting in a physiologically less expensive development of dermal scales. Both dorsal and gastral scales of early tetrapods consist uniformly of parallel fibred bone with circumferential growth marks (Dias & Richter 2003; Witzmann 2011 **[9])**, and the thick basal layer consisting of isopedine is completely reduced.

The well-ossified rhombic and spindle-shaped gastral scales indicate that the integument was initially very thick in early tetrapods. This is also supported by the dorsal, round-oval scales that were originally cup-shaped and thick in most Carboniferous and Early Permian early tetrapods. Many derived Late Permian and Triassic forms (i.e. stereospondyls) have less ossified, thinner gastral and dorsal scales or have even reduced dermal scales completely. This might indicate that the integument has become proportionally thinner in these forms (Witzmann 2007 **[8]**). The conspicuous, deep lateral line sulci on the skull roofing bones of most stereospondyls with reduced scales support this interpretation. In contrast, the lateral line sulci of most aquatic Palaeozoic temnospondyls with thick dermal scales are comparatively weakly impressed on the skull bones, and consist of long oval depressions that are sometimes difficult to distinguish from the furrows of the dermal sculpture. One may conclude that the lateral lines left only weak traces on the bones because the integument was proportionally thicker, whereas in the forms with the possibly thinner integument the lateral lines came to lie on the surface of the bones.

3. The hyobranchial apparatus in early tetrapods and its significance for feeding and breathing

3.1 The configuration of the hyobranchial apparatus during the fish-to-tetrapod transition

3.1.1 Introduction

The hyobranchial apparatus shows a wide variety of morphologies and characteristics among the different lineages and taxa of jaw-bearing fishes and tetrapods. Figure 8 shows the schematic reconstruction of the hyobranchial apparatus of a "generalised" early vertebrate. The plesiomorphic configuration of the hyobranchial skeleton is a complex set of paired segmented arches, consisting of the mandibular arch (i.e., the jaws), followed by the hyoid arch and the subsequent branchial (or gill) arches, which are linked ventrally to the median basibranchial series (Nelson 1969; Janvier 1996). Whereas the mandibular arch consists of only two segments (palatoquadrate dorsally and Meckelian cartilage ventrally), the hyoid arch can be subdivided (from ventral to dorsal) into basihyal, hypohyal, ceratohyal and hyomandibula (the stapes of tetrapods). The posteriorly following gill arches may vary from one to six in jaw-bearing fishes and tetrapods. The following segments can be distinguished per gill arch (from ventral to dorsal): hypo-, cerato-, epi-, and pharyngobranchial. The gills (either external or internal gills or both) are attached to the gill arches, more precisely the ceratobranchials. This chapter seeks to reconstruct what is the plesiomorphic condition of the hyobranchial apparatus in early tetrapods, and which changes occurred in this skeletal region in the fish-to-tetrapod transition.

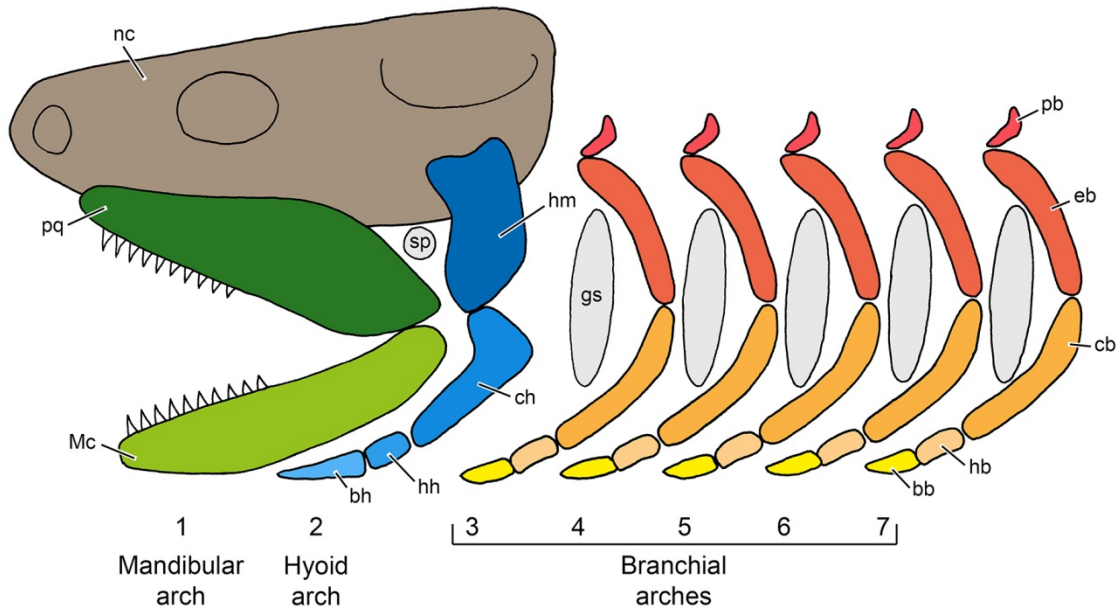

Figure 8: Schematic reconstruction of the "generalised" hyobranchium of an early vertebrate. Redrawn after Liem *et al.* (2001). **Abbreviations: bb,** basibranchial; **bh,** basihyal; **cb,** ceratobranchial; **eb,** epibranchial; **gs,** gill slit; **hb,** hypobranchial; **hh,** hypohyal; **ch,** ceratohyal; **hm,** hyomandibula; **nc,** neurocranium; **Mc,** Meckelian cartilage (lower jaw); **pb,** pharyngobranchial; **pq,** palatoquadrate (upper jaw); **sp,** spiraculum.

3.1.2 The plesiomorphic condition of the hyobranchial apparatus in early tetrapods

Comparison between the hyobranchial skeleton of tetrapodomorph fishes (Jarvik 1954, 1963; Lebedev 1995; Johanson & Ahlberg 1997; Long *et al.* 1997; Downs *et al.* 2008) and early tetrapods reveals the following picture. In tetrapodomorph fishes, an anterior and posterior basibranchial of rectangular to polygonal outline are present that are well ossified and have extensive articulation facets for the hypohyals and the first two pairs of hypobranchials. In early tetrapods, in contrast, only a single, poorly ossified basibranchial is present that is rod-like and has no ossified articulation facets. Where known, the hypohyals are much smaller elements in early tetrapods than in their fish-like relatives. Whereas the ceratohyal consists of an anterior and posterior element in many tetrapodomorph fishes, it is a single elongate element from *Tiktaalik* crown wards. In tetrapodomorph fishes, the four pairs of hypobranchials are stout elements and differentiated with crests and furrows. In early tetrapods, these elements are simplified and rod-like, and albeit there is a trend to reduce the hypobranchials to two pairs, their number is subject to variation within the different groups of early tetrapods. As in tetrapodomorph fishes, the plesiomorphic number of ceratobranchials is four pairs in early tetrapods, and they are similar in their curved shape and the posterolateral grooves (that housed the gill arteries, see chapter 3.2.2). The pharyngo- and epibranchials of fishes, which are located distal to the ceratobranchials, have never been demonstrated in tetrapods, and the only early tetrapods with unequivocal epibranchials preserved are *Acanthostega* (Clack & Coates 1993; Witzmann 2013 **[10]**) and among lepospondyls the microsaur *Pantylus*. Denticulate ossified platelets (or branchial teeth) in the pharyngeal region are present in tetrapodomorph fishes on almost all hyobranchial elements and the neurocranium. In early tetrapods, the denticulate platelets are restricted to the ceratobranchials to which they were attached (Schoch 2002; Witzmann 2004). Curiously, denticulate platelets have not been found in stem-amniotes with the exception of the microsaur *Microbrachis* (Olori 2013). Extant lissamphibians have completely reduced the teeth on the gill arches; however, larvae of early crown-group salamanders still developed teeth on the gill arches (Gao & Shubin 2012; Skutschas & Gubin 2012). Instead of branchial teeth, larvae of extant salamanders have gill rakers consisting of cartilage or connective tissue on the gill arches. These gill rakers may mineralise in rare cases and “resemble a tooth crown”, as reported in larvae of the salamander, *Rhyacotriton olympicus* (Worthington & Wake 1971, p. 358).

In conclusion, the basic arrangement of hyobranchial skeletal elements has been conserved to a considerable degree across the fish-to-tetrapod transition. Most changes in the hyobranchium during the fish-to-tetrapod transition encompass solely the reduction in number of skeletal elements and their morphological simplification. The plesiomorphic condition of the tetrapod hyobranchium can be reconstructed as follows: a single slender, rod-like basibranchial bone with expanded anterior and less expanded posterior portions, a pair of small, stout hypohyals, one pair of elongate, albeit flattened ceratohyals, four pairs of rod-like hypobranchials, four pairs of curved, deeply grooved ceratobranchials that bear elongate, denticulate branchial platelets, and short epibranchials.

3.2 Gill breathing in early tetrapods

3.2.1 Introduction

Lungs are phylogenetically ancient organs that evolved in the osteichthyan stem-group well before the first sarcopterygians invaded the land (Janvier 1996); the first tetrapods are therefore considered to have possessed lungs. Despite of the importance of aerial respiration, the majority of early tetrapods are likely to have had an aquatic existence (Schoch 2009). What

might have been the alternative to lung breathing in these early aquatic tetrapods? Extant lissamphibians are the only model for physiological inference: many of them use larval gills to breathe under water, but also cutaneous respiration is significant in numerous species, both terrestrial and aquatic (Duellman & Trueb 1986). Cutaneous respiration is difficult to prove in fossil taxa; however, both the inferred skin structure and the extensive cover of dermal scales in most early tetrapods and their often large overall body size make a large-scale contribution of the skin to breathing unlikely (see chapter 2.1.7). Therefore, the role of the gills in early tetrapods comes sharply into focus. While internal gills are essential organs in all jaw-bearing fishes, no living tetrapod retains them, even as vestiges. Instead, gills of a different kind are found in larvae of lissamphibians: instead of being located inside a gill chamber as in fishes, these gills are located outside the body surface and often form branching, bushy structures (Duellman & Trueb 1986). The homology of the external gills of amphibians and the internal gills of fishes has often been questioned. These observations raise the issue of identifying the type of gills (if any) present in those taxa that spanned the fish-to-tetrapod transition. In the Devonian stem-tetrapods *Acanthostega* and *Ichthyostega*, the retention of internal gills has been inferred from the structure of their bony gill arch skeleton (Coates & Clack 1991; Clack 2012). Presently, the (implicit) consensus seems to be that internal gills were lost after the branching of *Ichthyostega*, but before the origin of crown-group tetrapods (amphibian- and amniote-lineages). The evolutionary origin of the lissamphibian-type external gills is unknown, but fossil evidence indicates that in several groups of Palaeozoic tetrapods, larval external gills similar to those of salamanders were present (Boy 1974; Klembara 1995; Witzmann 2004). In conclusion, there must have been a phase in which the internal gills disappeared and the external ones evolved. It is unknown whether this involved a transformation from one gill type into another, or if one truly disappeared and was replaced by a completely new and convergent structure. So what do the fossils tell?

3.2.2 Osteological correlates of internal gills

A review of the hyobranchial apparatus in early tetrapods reveals that the branchial or gill arches (i.e. ceratobranchials) may bear important osteological correlates of soft anatomical structures. First-hand examination of extant sarcopterygian fishes (the coelacanth *Latimeria* and the Australian lungfish *Neoceratodus*) and extant actinopterygians confirm the reliability of these correlates (Schoch & Witzmann 2011 **[11]**). These are: (1) grooves on the posterolateral flank of the ceratobranchials indicating the presence of gill arteries, and (2) a postbranchial lamina on the shoulder girdle (clavicle and cleithrum) indicating the presence of a gill chamber. Therefore, internal gills similar to those of *Latimeria* and *Neoceratodus* are likely to have existed in taxa possessing such grooved ceratobranchials. In contrast to internal gills of fishes, the gill arteries of the external gills of lissamphibian larvae are not located in close neighbourhood to the gill arches; thus, ceratobranchials with external gills are not grooved as those with internal gills. The osteological features correlated with internal, fish-like gills are more widespread among Palaeozoic and Mesozoic early tetrapods than previously thought. According to these findings, internal gills were not only present in the earliest tetrapods of the Devonian (Coates & Clack 1991; Clack *et al.* 2003), but also in Carboniferous stem-tetrapods and present in a range of adult, aquatic temnospondyls (Schoch & Witzmann 2011 **[11];** Witzmann 2013 **[10]**).

Direct preservation of external gills is reported in a range of early crown-group tetrapods, confirming earlier views (Witzmann 2004) that they must have been present in (at least the larval stages of) the earliest crown tetrapods. These external gills resemble those of basal salamanders and are probably their phylogenetic precursors. The question whether early tetrapods had internal or external gills can be resolved by examination of osteological features.

The results suggest that the distribution of internal and external gills is different from what was thought before: internal gills did not disappear before the external ones evolved. This parallels the situation in lepidosirenid lungfishes: in the South American lungfish *Lepidosiren* and the African lungfish *Protopterus*, both larval external gills and adult internal gills are present. In early tetrapods, this appears to have occurred convergently to lungfishes (Schoch & Witzmann 2011 **[11]**). Among early crown-group tetrapods, internal gills may have been present among "anthracosaurs" in embolomeres (stem-amniotes), since Pawley (2006) reported a postbranchial lamina in *Archeria*. Taking the analyses of Ruta & Coates (2007) and Schoch (2013) as phylogenetic framework, then internal gills were reduced at least twice in tetrapod evolution: in temnospondyls the clade comprising the terrestrial zatracheids and dissorophoids (the latter giving rise to lissamphibians) and on the amniote stem below lepospondyls and seymouriamorphs (Witzmann 2013 **[10]**). External gills developed somewhere on the tetrapod stem and were retained in temnospondyls (including lissamphibians) and were reduced on the amniote stem in the immediate ancestors of amniotes.

3.2.3 The question of homology of internal and external gills

In jaw-bearing fishes, the lamellae of internal gills are long, vascularised sheets of tissue in which the respiratory gas exchange takes place (Sewertzoff 1924; Rauther 1937). They form numerous parallel, closely spaced lobes attached to the posteroventral flank of the gill arches. The lamellae are clearly separated from the septum which divides the anterior and posterior lamellae of each gill arch. Gill septa are layers of connective tissue that separate the anterior and posterior gill lamellae of each gill arch. The septa of sarcopterygian fishes (*Latimeria*, *Neoceratodus*) are as long as the lamellae, whereas in actinopterygians, the septa are usually shorter or even rudimentarily developed. As the internal gills of fishes, the external gills of lissamphibian larvae are attached to the ceratobranchials. However, in contrast to the fish condition, the gill lamellae are not attached to the ceratobranchial, but arise from the gill septum proper, which is probably homologous to that of jaw-bearing fishes. The distal edge of the septum is serrated to form gill lamellae that are very similar to the ones of internal gills. If the enlarged septum of sarcopterygian fishes and lissamphibian larvae is indeed a shared-derived character of sarcopterygians, then the formation of lamellae at the end of the septum would only be a final step towards the lissamphibian condition. Hence, external gills could be derived from internal ones, although the lamellae themselves are probably not homologous (Schoch & Witzmann 2011 **[11]**).

3.3 The hyobranchial apparatus and feeding in early tetrapods

3.3.1 Introduction

Apart from breathing, the hyobranchial apparatus of jaw-bearing fishes plays a pivotal role in aquatic feeding. Movements of the apparatus assist in opening the jaws and expanding the bucco-pharyngeal cavity, thus generating negative pressure within the mouth cavity and initiating a rapid inflow of water together with the prey, a process called suction feeding (Deban & Wake 2000). Because air is a much less dense medium than water, the hyobranchial apparatus of fishes and aquatic early tetrapods had to be remodelled during the change from an aquatic to a rather terrestrial existence in order to support and move a fleshy tongue that manipulates and transports the prey in the oral cavity (Wake & Deban 2000). This chapter will focus on determining if it is possible to distinguish between an "aquatic" and a "terrestrial" hyobranchial apparatus in early tetrapods. In other words, what is the evidence in hyobranchial morphology for suction feeding in aquatic forms, and is it possible to identify remodelling of

the hyobranchium for tongue-based feeding on land in terrestrial forms?

3.3.2 Hyobranchium and suction feeding in early tetrapods: a case study of the plagiosaurid Gerrothorax

In the rich fossil material of the Triassic plagiosaurid stereospondyl *Gerrothorax*, numerous traces of muscle attachments can be identified on the skull and the well ossified, "fish-like" hyobranchial apparatus including four pairs of grooved ceratobranchials (Fig. 9). The objective of this paragraph is to achieve a comprehensive understanding of the feeding apparatus in this fully aquatic early tetrapod. Cranial and hyobranchial muscles were reconstructed as far as possible, based on direct evidence (spatial limitations, ossified muscle insertion sites on skull, mandible, and hyobranchium) and on phylogenetic reasoning (with extant basal actinopterygians and salamanders as bracketing taxa). The resulting skeletal and soft-anatomical data were used as a basis for an integrated functional hypothesis of prey capture in *Gerrothorax* (Witzmann & Schoch 2013 **[12]**).

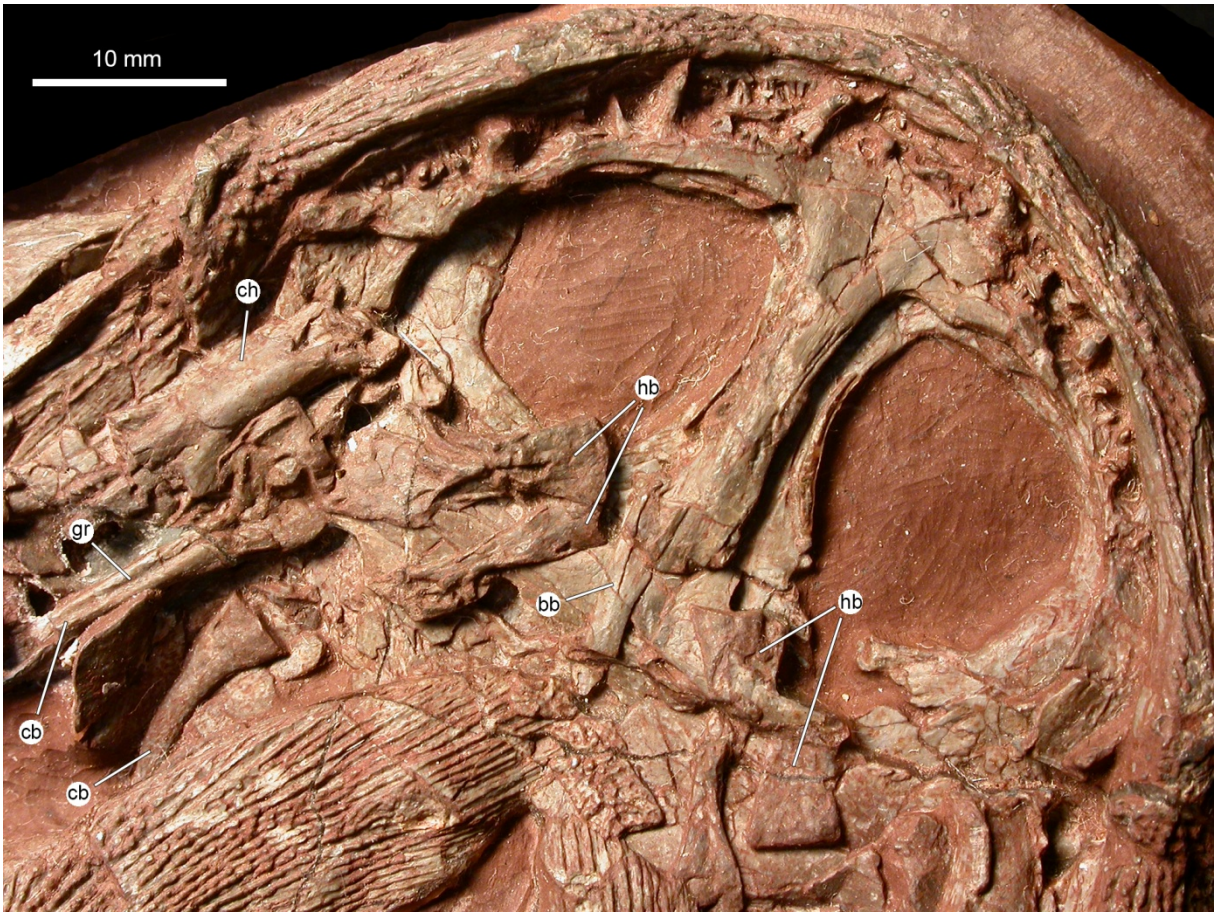

Figure 9: Skull and hyobranchial apparatus of the stereospondylomorph temnospondyl *Gerrothorax pulcherrimus* from the Late Triassic of Greenland in ventral view (MGUH 28919). **Abbreviations: bb,** basibranchial; **cb,** ceratobranchial; **ch,** ceratohyal; **gr,** groove on ceratobranchial; **hb,** hypobranchial; **MGUH,** Geological Museum, University of Copenhagen, Denmark.

***Morphological evidence for suction feeding in* Gerrothorax.** Previous studies on temnospondyl feeding largely neglected the role of the hyobranchial apparatus during feeding (e.g., Panchen 1959; Howie 1970; Jenkins *et al.* 2008). As this apparatus is extensively ossified in *Gerrothorax* and bears prominent muscle attachment sites, it must be assumed that it was

involved in capture of prey under water, more specifically, in expansion of the buccal cavity and thus in suction feeding. The following aspects of skull and hyobranchial morphology indicate that *Gerrothorax* was able to prey by suction feeding in water: the broad, short-faced skull, which is a prerequisite for suction feeding (Taylor 1987); the broad, anteriorly directed mouth opening (enabling directed flow of water into the buccal cavity); the robust, well ossified hyobranchial apparatus which is required to generate strong suction (Deban & Wake 2000). Furthermore, strong associated hyobranchial muscles are necessary for suction feeding, and at least a strong m. rectus cervicis can be reconstructed in *Gerrothorax* that was able to draw the hyobranchium rapidly in a posteroventral direction (see below). The internal gills as indicated by grooved ceratobranchials (see chapter 3.2.2) and the associated branchial denticles (Nilsson 1946; Witzmann 2013 **[10]**) indicate a water-filled pharynx by analogy with extant osteichthyans.

Reconstruction of the feeding strike of **Gerrothorax.** The flattened morphology, the short limbs and tail and the heavily built skeleton including an extensive cover of osteoderms (see chapter 2.2) strongly suggest that *Gerrothorax* was a bottom-dwelling ambush predator in freshwater and brackish environments (Hellrung 2003; Jenkins *et al.* 2008; Schoch & Witzmann 2012). However, if *Gerrothorax* rested on the bottom during prey capture and solely raised the head as suggested by Jenkins *et al.* (2008), there would have been by far not enough interspace between skull and pectoral girdle to retract the hyobranchial apparatus and to increase the size of the buccal cavity for suction feeding. Furthermore, the muscle scars on the postglenoid area of the mandible indicate that one of the two portions of the m. depressor mandibulae extended backwards on the back of the trunk behind the skull. This suggests that the depressor was indeed used for lowering the mandible and not to raise the skull as earlier supposed (Panchen 1959) and implies that the skull including the mandible must have been lifted off the ground during prey capture. It can thus be assumed that when bypassing prey was recognised by *Gerrothorax*, it raised the head (and possibly also the anterior trunk region) toward the prey with the jaws still closed. Then the mouth started to open rapidly. This was caused by (1) raising the head as shown by the extant bracketing taxa basal osteichthyans (Lauder 1980), extant lungfishes (Bemis 1986) and aquatic salamanders (Lauder & Shaffer 1985), by action of strong epaxial muscles (strong muscle attachment sites are visible on the occiput and occipital lamellae of the skull table in *Gerrothorax*) and probably the cleidomastoideus muscle (that is supposed to have linked the cleithrum and the region of the tabular in at least some stereospondyls, see Howie 1970; Shiskin 1987; Sulej & Majer 2005; Jenkins *et al.* 2008), and (2) by lowering the mandible by action of the strong m. depressor mandibulae and the m. rectus cervicis. During further elevation of the skull, the action of the m. rectus cervicis rotated the hyobranchial apparatus ventrally and caudally, thus expanding the buccal cavity and causing the inflow of water plus prey through the mouth opening. The obviously strong m. depressor mandibulae, the well ossified, large quadrate-articular joint and the powerful m. rectus cervicis (which in *Gerrothorax* inserted on a distinct crest on the prominent first hypobranchial and was attached posteriorly on the large interclavicle) suggest that this action occurred rapidly and that strong suction was generated. As bracketing by extant basal osteichthyans and salamander larvae (Lauder 1980; Lauder & Reilly 1994) suggests, maximum hyobranchial retraction occurred after maximum gape. The m. geniohyoideus (that originated on a posterior attachment site of the mandibular symphysis in *Gerrothorax* and might have inserted on the elaborate first hypobranchial) pulled the hyobranchium anterodorsally, and water was expelled through the opened gill clefts. The captured prey item was seized by pressure of the hyobranchial apparatus against the palate (the parasphenoid is toothed in at least some individuals of *Gerrothorax*; Schoch & Witzmann 2012) and was probably moved toward the oesophagus by a posteriorly directed current of water as in larvae of salamanders as well as in actinopterygians and lungfishes (Lauder & Reilly 1994). The

denticulate branchial platelets situated on the ceratobranchials prevented the prey from escaping through the gill clefts. Similar to the jaw opening muscles, also the jaw adductors were well developed as indicated by osteological correlates on the ventral side of the dermal skull roof, the palate and on the mandible, enabling a rapid closure of the mouth. Despite the similarities of the feeding mechanism in *Gerrothorax* to that in extant salamander larvae, a striking difference exist: unlike in extant salamander larvae and many derived actinopterygians (teleosts), no cranial kinesis was possible in the *Gerrothorax* skull, because all sutures of skull roof and palate are rigid and no moveable articulation of skull bones was present, neither in the skull roof nor in the palate. An akinetic skull roof is characteristic for the vast majority of temnospondyls and is probably plesiomorphic for early tetrapods in general; in this respect, the skull of *Gerrothorax* and most temnospondyls resemble those of extant basal actinopterygians (Lauder 1980; Janvier 1996).

3.3.3 Hyobranchium and aquatic feeding in non-suction feeding early tetrapods

In contrast to limbed stem-tetrapods like adelogyrinids, or temnospondyls like dvinosaurians, plagiosaurids, and brachyopids that have well ossified hyobranchia including ossified gill arches proper, the hyobranchial apparatus remained largely cartilaginous in a great number of aquatic early tetrapods, and most often, only the rod-like basibranchial (and casually also the associated hypobranchials) was ossified. Examples for this situation are colosteids and many stereospondylomorph temnospondyls. However, three to four rows of branchial platelets in the throat region indicate that the posterior gill arches were still present and fish-like, albeit cartilaginous, elements. The fact that from the hyobranchial apparatus only the basibranchial was ossified in several taxa of aquatic early tetrapods might be connected with the functional role of this element as point of insertion of the m. rectus cervicis: this muscle aids in lowering the mandible when pulled posteroventrally in larval salamanders (see chapter 3.3.2), a mechanism that is probably plesiomorphic for jaw-bearing vertebrates (Lauder & Reilly 1994). Additionally, the rigid basibranchial bone served for pressing the prey against the toothed palate to seize and to manipulate it. Especially the elaborated, downturned anterior extension of the basibranchial in basal stereospondylomorphs may have served for insertion of a powerful m. rectus cervicis. In more derived stereospondylomorphs, the stereospondyls, a retroarticular process is often well developed on the mandibles and thus a strong m. depressor mandibulae is able to insert on the lower jaw (Schoch & Milner 2000). This development in stereospondyls might be correlated with a morphological simplification (and the frequent non-ossification) of the basibranchial. The absence of ossified gill arches and the elongate or parabolic skull shape in these early tetrapods suggests that they were “crocodilomorph” feeding analogues (Damiani 2001; Witzmann 2006; Fortuny *et al.* 2011), that is, they used rapid sidewards sweeps of the head and direct biting, rather than elaborate suction feeding.

3.3.4 Hyobranchium and terrestrial feeding in early tetrapods

The adult hyobranchial apparatus of most primarily terrestrial early tetrapods is almost unknown, probably because the hyobranchium remained largely cartilaginous. In contrast, the larval hyobranchium of many of these forms is well known based on the presence of ossified or cartilaginous branchial arches often associated with branchial dentition and external gills (Boy 1974; Witzmann 2004). What can we reconstruct from the adult “terrestrial” hyobranchial apparatus in early tetrapods in spite of this rather frustrating scarceness of data?

Interestingly, there is evidence that the third or even the fourth gill arch (and thus a “fish-like” hyobranchium) was retained not only in primarily aquatic early tetrapods, but also in rather terrestrial forms like the microsaur *Pantylus* (Romer 1969), although internal and

external gills were certainly absent in the terrestrial adults. Also the anteroventral hyobranchial elements (basibranchial, ceratohyals, hypobranchials) of terrestrial adult dissorophoid temnospondyls like *Micropholis* (Boy 1985; Witzmann 2013 **[10]**), *Pasawioops* (Fröbisch & Reisz 2008) and *Doleserpeton* (Sigurdsen & Bolt 2010) resemble closely the elements in the "aquatic" type hyobranchium (unfortunately, however, the ceratobranchials are not preserved in adult dissorophoids). Evidence of a transformation or remodelling into a true "terrestrial" hyobranchium (i.e., with the posterior gill arches reduced and the anteromedial hyobranchial elements modified to support a moveable tongue for terrestrial feeding) is poor in early tetrapods and evidence for this has so far been reported only in two taxa. In larvae of the zatracheid temnospondyl *Acanthostomatops*, Witzmann & Schoch (2006 **[13]**) showed four pairs of ossified gill arches that do not bear posterolateral grooves; thus, no internal (but probably external) gills were present in the living animal. The largest (adult) specimen lacks any ceratobranchials. Instead, it preserves a full range of rather delicate, rod- and plate-like bones ventral to the anterior part of the parasphenoid basal plate. One may conclude that during ontogeny of *Acanthostomatops*, the larval hyobranchial apparatus was reorganised in larger specimens, including resorption of ceratobranchials and ossification of the anteroventral portion of the hyobranchial skeleton. Thus, a "larval" gill-supporting skeleton apparently transformed into an "adult" tongue-supporting apparatus in *Acanthostomatops*. This fits into the concept that in zatracheids, an enlarged intermaxillary gland (as indicated by a large fontanelle in the snout region) played a key role in terrestrial feeding (Schoch 1997). On the basis of the blade-like ceratohyal reminiscent to those of metamorphosed salamanders, Clack & Milner (2010) suspected that the otherwise not preserved adult hyobranchial skeleton in the dissorophoid *Platyrhinops* represents a primitive version of the tongue-elevating system found in salamanders.

Based on the admittedly very incomplete preservation of the hyobranchium in primarily terrestrial early tetrapods one may tentatively conclude that the first tetrapods feeding on land performed jaw prehension (i.e. simple closure of the mouth around the prey during which the hyobranchial apparatus plays a little role) rather than tongue-based feeding and still retained three or four pairs of gill arches. Because metamorphosed, terrestrial caecilians retain three or four pairs of gill arches, have a poorly developed tongue musculature and use jaw prehension for terrestrial prey capture (Stadtmüller 1936; Wake 1989; O'Reilly 2000), they might serve as an extant analogue among lissamphibians (although they possess a highly derived jaw closing mechanism, and it is not clear if they have reduced a tongue-supporting apparatus secondarily). On the lissamphibian stem (dissorophoids) tongue-based feeding might have started in *Platyrhinops*-like forms, giving rise to terrestrial feeding by tongue-protraction in lissamphibians, and this might have evolved convergently in zatracheids. On the amniote lineage, the situation is even more ambiguous, and the fossil record gives no evidence of when and how often a "terrestrial" hyobranchial apparatus evolved in early amniotes and their immediate stem-forms.

4. Conclusions and outlook

Although dermal bone histology and fossil integumentary structure were thoroughly studied in fossil amniotes in recent years, see e.g. de Ricqlès *et al.* (2001), Scheyer & Sander (2004), Main *et al.* (2005), Hill (2005, 2006), Scheyer (2007), Scheyer & Sánchez-Villagra (2007) and Scheyer & Anquetin (2008), this topic has so far received the attention of only few workers in early tetrapods. Similarly, the role of the hyobranchial apparatus in feeding and breathing of early tetrapods has often been underestimated. This may be due to the fact that the sometimes tiny and feebly ossified hyobranchial skeletal elements of early tetrapods are often poorly preserved and are thus difficult to interpret. This thesis has tried to show that many inferences concerning associated soft-parts (like soft-tissue integument, gills and muscles) that are important to understand the way of life and physiology can be drawn also from early tetrapod dermal bone structure and the gill skeleton. In some of these aspects, like the hyobranchial apparatus, early tetrapods were remarkably conservative and fish-like. Other characters, like the scalation pattern, appear to have evolved very quickly during the fish-to-tetrapod transition.

The data presented here naturally do not represent the ultimate answers to early tetrapod integumentary structure, their hyobranchial apparatus and associated functions. There are a number of problems that could guide future studies on the subject. For instance, future work on extant tetrapods may yield histological and / or chemical signatures that can be applied to fossil sculptured dermal bones, to test the hypothesis that dermal sculpture had the function of buffering acidosis. Furthermore, also the dermal scales of stem-amniotes and early amniotes should be in-depth investigated morphologically and histologically, to clarify the proposed homology of gastral scales and amniote gastralia (see e.g. Claessens 2004). Concerning the gills of sarcopterygians, it would be of interest to trace the fate of cells that give rise to the gill septum, gill lamellae and arteries in both sarcopterygian fishes and salamander larvae. Only developmental studies can reveal (a) the homology of tissue layers in the gill region, (b) the mechanisms of gill formation and (c) form the basis for a model of how – and why – internal gills evolved into external ones. A further unresolved problem is the question of homology of the medial elements in the larval hyobranchium of salamanders and caecilians (i.e. basibranchials, basihyal, urohyal) with respect to the hyobranchium in early tetrapods and tetrapodomorph fishes. Morphological and histological investigation of the "mineralised gill rakers" and their morphogenesis in larvae of the extant salamander *Rhyacotriton olympicus* (Worthington & Wake 1971) and comparisons with the similarly arranged branchial teeth of branchiosaurids and early salamanders (Gao & Shubin 2012; Skutschas & Gubin 2012) might yield important data to test the hypothesis that the Permo-Carboniferous branchiosaurids and caudates are sister groups (Carroll 2004, 2007), and might shed light on the origin of salamanders.

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6. References

(Contributions that are part of this habilitation thesis are emphasised in bold)

Ahlberg, P. E., Clack, J. A. & Blom, H. 2005. The axial skeleton of the Devonian tetrapod *Ichthyostega*. – Nature 437: 137–140.

Bemis, W. E. 1986. Feeding systems of living Dipnoi: Anatomy and function. – Journal of Morphology 190 (Supplement 1): 249–275.

Boy, J. A. 1974. Die Larven der rhachitomen Amphibien (Amphibia: Temnospondyli; Karbon – Trias). – Paläontologische Zeitschrift 48: 236–282.

Boy, J. A. 1985. Über *Micropholis*, den letzten Überlebenden der Dissorophoidea (Amphibia, Temnospondyli; Unter-Trias). – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1985: 29–45.

Boy, J. A. 1988. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstes Karbon-Perm). 1. *Sclerocephalus*. – Paläontologische Zeitschrift 62: 107–132.

Boyde, A. 1972. Scanning electron microscopic studies of bone. *In* Bourne, G. (ed.). The biochemistry and physiology of bone, vol. 1. Academic Press, New York: pp. 259–309.

Brazeau, M. D. & Ahlberg, P. E. 2006. Tetrapod-like middle ear architecture in a Devonian fish. – Nature 439: 318–321.

Buchwitz, M. & Voigt, S. 2010. Peculiar carapace structure of a Triassic chroniosuchian implies evolutionary shift in trunk flexibility. – Journal of Vertebrate Paleontology 30: 1697–1708.

Buchwitz, M., Witzmann, F., Voigt, S. & Golubev, V. 2012. Osteoderm microstructure indicates the presence of a crocodylian-like trunk bracing system in a group of armoured basal tetrapods. – Acta Zoologica (Stockholm) 93: 260–280.

Buffrénil, V. de 1982. Morphogenesis of bone ornamentation in extant and extinct crocodilians. – Zoomorphologie 99: 155–166.

Bystrow, A. P. 1935. Morphologische Untersuchungen der Deckknochen des Schädels der Wirbeltiere. 1. Mitteilung. Schädel der Stegocephalen. – Acta Zoologica (Stockholm) 16: 65–141.

Bystrow, A. P. 1947. Hydrophilous and xerophilous labyrinthodonts. – Acta Zoologica (Stockholm) 28: 137–164.

Carroll, R. L. 2004. The importance of branchiosaurs in determining the ancestry of the modern amphibian orders. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 232: 157–180.

Carroll, R. L. 2007. The Palaeozoic ancestry of salamanders, frogs and caecilians. – Zoological Journal of the Linnean Society 150 (Supplement 1): 1–140.

Castanet, J., Francillon-Vieillot, H., Ricqlès, A. de & Zylberberg, L. 2003. The skeletal histology of the Amphibia. *In* Heatwole, H. & Davies, M. (eds). Amphibian Biology, vol. 5: Osteology. Surrey Beatty & Sons, Chipping Norton: pp. 1598–1683.

Clack, J. A. 1992. The stapes of *Acanthostega gunnari* and the role of the stapes in early tetrapods. *In* Webster, D. B., Fay, R. R. & Popper, A. N. (eds). Evolutionary biology of hearing. Springer-Verlag, New York: pp. 405–420.

Clack, J. A. 2006. The emergence of early tetrapods. – Palaeogeography, Palaeoclimatology, Palaeoecology 232: 167–189.

Clack, J. A. 2009. The fin to limb transition: new data, interpretations, and hypotheses from paleontology and developmental biology. – Annual Review of Earth and Planetary Sciences 37: 163–179.

Clack, J. A. 2012. Gaining Ground. Second edition. Indiana University Press, Bloomington, Indiana.

Clack, J. A. & Coates, M. I. 1993. *Acanthostega gunnari* - our present connection. *In* Hoch, E. & Brantsen, A. K. (eds). Deciphering the natural world and the role of museums and collections. Geologisk Museum Press, Copenhagen: pp. 39–42.

Clack, J. A. & Finney, S. 2005. *Pederpes finneyae*, an articulated tetrapod from the Tournaisian of western Scotland. – Journal of Systematic Palaeontology 2: 311–346.

Clack, J. A. & Klembara, J. 2009. An articulated specimen of *Chroniosaurus dongusensis*, and the morphology and relationships of the chroniosuchids. – Special Papers in Palaeontology 81: 15–42.

Clack, J. A. & Milner, A. R. 2010. Morphology and systematics of the Pennsylvanian amphibian *Platyrhinops lyelli* (Amphibia: Temnospondyli). – Transactions of the Royal Society of Edinburgh: Earth Sciences 100: 275–295.

Clack, J. A, Ahlberg, P. E., Finney, S. M., Dominguez Alonso, P., Robinson, J. & Ketcham, R. A. 2003. A uniquely specialized ear in a very early tetrapod. – Nature 425: 65–69.

Claessens, L. P. A. M. 2004. Dinosaur gastralia; origin, morphology, and function. – Journal of Vertebrate Paleontology 24: 89–106.

Coates, M. I. & Clack, J. A. 1991. Fish-like gills and breathing in the earliest known tetrapod. – Nature 352: 234–236.

Daeschler, E. B., Shubin, N. H. & Jenkins, F. A. 2006. A Devonian tetrapod-like fish and the evolution of the

tetrapod body plan. – Nature 440: 757–763.
Damiani, R. J. 2001. Cranial anatomy of the giant Middle Triassic temnospondyl *Chernia megarhina* and a review of feeding in mastodonsaurids. – Palaeontologica Africana 37: 41–52.
Deban, S. M. & Wake, D. B. 2000. Aquatic Feeding in Salamanders. *In* Schwenk, K. (ed.). Feeding: form, function and evolution in tetrapod vertebrates. Academic Press, San Diego: pp. 65–94.
DeMar, R. 1966. The phylogenetic and functional implications of the armor of the Dissorophidae. – Fieldiana: Geology 16: 55–88.
DeMar, R. 1968. The Permian labyrinthodont amphibian *Dissorophus multicinctus*, and adaptations and phylogeny of the family Dissorophidae. – Journal of Paleontology 42: 1210–1242.
Dias, E. V. & Richter, M. 2003. On the squamation of *Australerpeton cosgriffi* Barberena, a temnospondyl amphibian from the Upper Permian of Brazil. – Anais da Academia Brasileira de Ciências 74: 477–490.
Dilkes, D. 2009. Comparison and biomechanical interpretations of the vertebrae and osteoderms of *Cacops aspidephorus* and *Dissorophus multicinctus* (Temnospondyli, Dissorophidae). – Journal of Vertebrate Paleontology 29: 1013–1021.
Dilkes, D. & Brown, L. E. 2007. Biomechanics of the vertebrae and associated osteoderms of the Early Permian amphibian *Cacops aspidephorus*. – Journal of Zoology 271: 396–407.
Downs, J. P., Daeschler, E. B., Jenkins, F. A. & Shubin, N. H. 2008. The cranial endoskeleton of *Tiktaalik roseae*. – Nature 455: 925–929.
Duellman, W. E. & Trueb, L. 1986. Biology of amphibians. Reprint 1994. Johns Hopkins University Press, Baltimore
Fortuny, J., Marcé-Nogué, J., de Esteban-Trivigno, S., Gil, L. & Galobart, À. 2011. Temnospondyli bite club: ecomorphological patterns of the most diverse group of early tetrapods. – Journal of Evolutionary Biology 24: 2040–2054.
Fröbisch, N. B. & Reisz, R. R. 2008. A new Lower Permian amphibamid (Dissorophoidea, Temnospondyli) from the fissure fill deposits near Richards Spur, Oklahoma. – Journal of Vertebrate Paleontology 28: 1015–1030.
Gao, Ke-Qin & Shubin, N. H. 2012. Late Jurassic salamandroid from western Liaoning, China. – Proceedings of the National Acandemy of Sciences 109: 5767–5772.
Gemballa, S. & Bartsch, P. 2002. Architecture of the integument in lower teleostomes: functional morphology and evolutionary implications. – Journal of Morphology 253: 290–309.
Golubev, V. K. 1998. Narrow-armored chroniosuchians (Amphibia, Anthracosauromorpha) from the Late Permian of Eastern Europe. – Paleontological Journal 32: 278–287.
Goodwin, M. B. & Horner, J. R. 2004. Cranial histology of pachycephalosaurs (Ornithischia: Marginocephalia) reveals transitory structures inconsistent with head-butting behavior. – Paleobiology 30: 252–267.
Gross, W. 1930. Die Fische des mittleren Old Red Süd-Livlands. – Geologische und Paläontologische Abhandlungen 22: 123–156.
Gross, W. 1966. Kleine Schuppenkunde. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 125: 29–48.
Haines, R. W. & Mohuiddin, A. 1968. Metaplastic bone. – Journal of Anatomy 103: 527–538.
Hellrung, H. 2003. *Gerrothorax pustuloglomeratus*, ein Temnospondyle (Amphibia) mit knöcherner Branchialkammer aus dem Unteren Keuper von Kupferzell (Süddeutschland). – Stuttgarter Beiträge zur Naturkunde, Serie B 330: 1–130.
Hill, R. V. 2005. Integration of morphological data sets for phylogenetic analysis of Amniota: the importance of integumentary characters and increased taxonomic sampling. – Systematic Biology 54: 1–18.
Hill, R. V. 2006. Comparative anatomy and histology of xenarthran osteoderms. – Journal of Morphology 267: 1441–1460.
Holmes, R. R., Carroll, R. L. & Reisz, R. R. 1998. The first articulated skeleton of *Dendrerpeton acadianum* (Temnospondyli, Dendrerpetontidae) from the Lower Pennsylvanian locality in Joggins, Nova Scotia, and a review of its relationships. – Journal of Vertebrate Paleontology 18: 64–79.
Howie, A. A. 1970. A new capitosaurid labyrinthodont from East Africa. – Palaeontology 13: 210–253.
Janis, C. M., Devlin, K., Warren, D. E. & Witzmann, F. 2012. Dermal bone in early tetrapods: a palaeophysiological hypothesis of adaptation for terrestrial acidosis. – Proceedings of the Royal Society of London, Series B 279: 3035–3040.
Janvier, P. 1996. Early Vertebrates. Reprint 2002. Oxford, Clarendon Press.
Jarvik, E. 1954. On the visceral skeleton in *Eusthenopteron* with a discussion of the parasphenoid and palatoquadrate in fishes. – Kungliga Svenska Vetenskapsakademiens Handlingar. Fjärde Serien, Band 5 (1): 1–104.
Jarvik, E. 1963. The composition of the intermandibular division of the head in fish and tetrapods and the diphyletic origin of the tetrapod tongue. – Kungliga Svenska Vetenskapsakademiens Handlingar. Fjärde Serien, Band 9 (1): 1–74.

Jenkins, F. A., Shubin, N. H., Gatesy, S. M. & Warren, A. A. 2008. *Gerrothorax pulcherrimus* from the Upper Triassic Fleming Fjord Formation of East Greenland and a reassessment of head lifting in temnospondyl Feeding. – Journal of Vertebrate Paleontology 28: 935–950.

Johanson, Z. & Ahlberg, P. E. 1997. A new tristichopterid (Osteolepiformes; Sarcopterygii) from the Mandagery Sandstone (Famennian) near Canowindra, N.S.W., Australia. – Transactions of the Royal Society of Edinburgh: Earth Sciences 88: 39–53.

Klembara, J. 1995. The external gills and ornamentation of skull roof bones of the Lower Permian tetrapod *Discosauriscus* (Kuhn 1933) with remarks to its ontogeny. – Paläontologische Zeitschrift 69: 265–281.

Lauder, G. V. 1980. Evolution of the feeding mechanism in primitive actinopterygian fishes: a functional anatomical analysis of *Polypterus*, *Lepisosteus* and *Amia*. – Journal of Morphology 163: 283–317.

Lauder, G. V. & Shaffer, B. H. 1985. Functional morphology of the feeding mechanism in Aquatic Ambystomatid Salamanders. – Journal of Morphology 185: 297–326.

Lauder, G. V. & Reilly, S. M. 1994. Amphibian feeding behavior: comparative biomechanics and evolution. *In* Bels, M., Chardon, P. & Vandewalle, P. (eds). Biomechanics of Feeding in Vertebrates. Advances in Comparative and Environmental Physiology, vol. 18. Springer-Verlag, Berlin: pp. 163–195.

Laurin, M. 2000. Seymouriamorphs. *In* Heatwole, H. & Carroll, R. L. (eds). Amphibian biology, vol. 4: Palaeontology. Surrey Beatty & Sons, Chipping Norton: pp. 1064–1080.

Laurin, M., Girondot, M. & Loth, M.-M. 2004. The evolution of long bone microstructure and lifestyle in lissamphibians. – Paleobiology 30: 589–613.

Lebedev, O. A. 1995. Morphology of a new osteolepidid fish from Russia. – Bulletin du Muséum National d'Histoire Naturelle. 4e Série. Section C. Sciences de la Terre. Paléontologie, Géologie, Minéralogie 17: 287–341.

Levrat-Calviac, V. & Zylberberg, L. 1986. The structure of the osteoderms in the gekko: *Tarentola mauritanica*. – American Journal of Anatomy 176: 437–446.

Liem, K., Bemis, W. E., Walker, W. F. & Grande, L. 2001. Functional anatomy of the vertebrates: an evolutionary perspective. Brooks/Cole Publishing, Pacific Grove, California.

Long, J. A., Barwick, R. E. & Campbell, K. S. W. 1997. Osteology and functional morphology of the osteolepiform fish *Gogonasus andrewsae* Long 1985, from the Upper Devonian Gogo Formation, Western Australia. – Records of the Western Australian Museum 53: 1–89.

Maddin, H. C., Musat-Marcu, S. & Reisz, R. R. 2007. Histological microstructure of the claws of the African Clawed Frog, *Xenopus laevis* (Anura: Pipidae): implications for the evolution of claws in tetrapods. – Journal of Experimental Zoology, Part B, Molecular and Developmental Evolution 308: 259–268.

Main, R. P., Ricqlès, A. de, Horner, J. R. & Padian, K. 2005. The evolution and function of thyreophoran dinosaur scutes: implications for plate function in stegosaurs. – Paleobiology 31: 291–314.

Marjanović, D. & Laurin, M. 2013. The origin(s) of extant amphibians: a review with emphasis on the "lepospondyl hypothesis". – Geodiversitas 35: 207–272.

Milner, A. R. 1990. The radiations of temnospondyl amphibians. *In* Taylor, P. D. & Larwood, G. P. (eds). Major Evolutionary Radiations. Systematics Association Special, vol. 42. Clarendon Press, Oxford: pp. 321–349.

Milner, A. R. & Sequeira, S. E. K. 1994. The temnospondyl amphibians from the Viséan of East Kirkton, West Lothian, Scotland. – Transactions of the Royal Society of Edinburgh, Earth Sciences 84: 331–361.

Mowbray, K. 2005. Surface bone histology of the occipital bone in humans and chimpanzees. – Anatomical Record, Part B 283: 14–22.

Nelson, G. J. 1969. Gill Arches and the Phylogeny of Fishes, With Notes on the Classification of Vertebrates. – Bulletin of the American Museum of Natural History 141: 477–552.

Niedźwiedzki, G., Szrek, P., Narkiewicz, K., Narkiewicz, M. & Ahlberg, P. E. 2010. Tetrapod trackways from the early Middle Devonian period of Poland. – Nature 463: 43–48.

Nilsson, T. 1946. A new find of *Gerrothorax rhaeticus* Nilsson, a plagiosaurid from the Rhaetic of Scania. – Lunds Universitets Årsskrift. N.F. 2, 42: 1–42.

Novikov, I. V. & Shishkin, M. A. 2000. Triassic chroniosuchians (Amphibia, Anthracosauromorpha) and the evolution of the trunk dermal ossifications in the bystrowianids. – Paleontological Journal 34 (Supplement): 165–178.

Novikov, I. V., Shishkin, M. A. & Golubev, V. K. 2000. Permian and Triassic anthracosaurs from Eastern Europe. *In* Shishkin, M., Benton, A. M. J., Unwin, D. M. & Kurochkin, E. N. (eds). The Age of Dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge: pp. 60–70.

O'Reilly, J. C. 2000. Feeding in caecilians. *In* Schwenk, K. (ed.). Feeding: form, function and evolution in tetrapod vertebrates. Academic Press, San Diego: pp. 149–166.

Olori, J. C. 2013. Ontogenetic sequence reconstruction and sequence polymorphism in extinct taxa: an example using early tetrapods (Tetrapoda: Lepospondyli). – Paleobiology 39: 400–428.

Ørvig, T. 1968. The dermal skeleton; general considerations. *In* Ørvig, T. (ed.). Current problems of lower

vertebrate phylogeny. Proceedings of the 4th Nobel Symposium. Almquist & Wiksell, Stockholm: pp. 373–397.
Panchen, A. 1959. A new armoured amphibian from the Upper Permian of East Africa. – Philosophical Transactions of the Royal Society of London, Series B 242: 207–281.
Pawley, K. 2006. The postcranial skeleton of temnospondyls (Tetrapoda: Temnospondyli). PhD dissertation, Faculty of Sciences, Technology, and Engineering, La Trobe University, Melbourne, Victoria.
Pierce, S., Ahlberg, P. E., Hutchinson, J. R., Molnar, J. L., Sanchez, S., Tafforeau, P. & Clack, J. A. 2013. Vertebral architecture in the earliest stem tetrapods. – Nature 494: 226-229.
Quinzio, S. & Fabrezi, M. 2012. Ontogenetic and Structural Variation of Mineralizations and Ossifications in the Integument within Ceratophryid Frogs (Anura, Ceratophryidae). – Anatomical Record 295: 2089–2103.
Rauther, M. 1937. Kiemen der Anamnier, Kiemendarmderivate der Cyclostomen und Fische. *In* Bolk, L., Göppert, E., Kallius, E. & Lubosch, W. (eds). Handbuch der vergleichenden Anatomie der Wirbeltiere, vol. 3. Urban & Schwarzenberg, Berlin: pp. 211–278.
Ricqlès, A. de, Pereda Superbiola, X., Gasparini, Z. & Olivero, E. 2001. Histology of dermal ossifications in an ankylosaurian dinosaur from the Late Cretaceous of Antarctica. – Asociación Paleontológica Argentina, Publicación Especial 7: 171–174.
Romer, A. S. 1969. The cranial anatomy of the Permian amphibian *Pantylus*. – Breviora 314: 1–37.
Romer, A. S. 1972. A Carboniferous labyrinthodont amphibian with complete dermal armor. – Kirtlandia 16: 1–8.
Ruibal, R. & Shoemaker, V. 1984. Osteoderms in anurans. – Journal of Herpetology 18: 313–328.
Ruta, M. & Coates, M. I. 2007. Dates, nodes and character conflict: addressing the lissamphibian origin problem. – Journal of Systematic Palaeontology 5: 69–122.
Salisbury, S. W. & Frey, E. 2000. A biomechanical transformation model for the evolution of semi-spheroidal articulations between adjoining vertebral bodies in crocodilians. *In* Grigg, G. C., Seebacher, F. & Franklin, C. E. (eds). Crocodilian Biology and Evolution. Surrey Beatty & Sons, Chipping Norton: pp. 85–134.
Scheyer, T. M. 2007. Skeletal histology of the armor of the Placodontia: the occurrence of "postcranial fibro-cartilaginous bone" and its developmental implications. – Journal of Anatomy 211: 737–753.
Scheyer, T. M. & Sander, P. M. 2004. Histology of ankylosaur osteoderms: implications for systematics and function. – Journal of Vertebrate Paleontology 24: 874–893.
Scheyer, T. M. & Sánchez-Villagra, M. R. 2007. Carapace bone histology in the giant pleurodiran turtle *Stupendemys geographicus*: phylogeny and function. – Acta Palaeontologica Polonica 52: 137–154.
Scheyer, T. M. & Anquetin, J. 2008. Bone histology of the Middle Jurassic turtle shell remains from Kirtlington, Oxfordshire, England. – Lethaia 41: 85–96.
Scheyer, T. M., Brüllmann, B. & Sánchez-Villagra, M. R. 2008. The ontogeny of the shell in side-necked turtles, with emphasis on the homologies of costal and neural bones. – Journal of Morphology 269: 1008–1021.
Schoch, R. R. 1997. Cranial anatomy of the Permian temnospondyl amphibian *Zatrachys serratus* Cope 1878, and the phylogenetic position of the Zatracheidae. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 206: 223–48.
Schoch, R. R. 2002. The evolution of metamorphosis in temnospondyls. – Lethaia 35: 309–327.
Schoch, R. R. 2009. The evolution of life cycles in early amphibians. – Annual Review of Earth and Planetary Sciences 37: 135–162.
Schoch, R. R. 2013. The evolution of major temnospondyl clades – an inclusive phylogenetic analysis. – Journal of Systematic Palaeontology, iFirst 2013.
Schoch, R. R. & Wild, R. 1999. Die Wirbeltier-Fauna im Keuper von Süddeutschland. *In* Hauschke, N. & Wilde, V. (eds). Die Trias – Eine ganz andere Welt. Verlag Dr. Friedrich Pfeil, München: pp. 395–408.
Schoch, R. R. & Milner, A. R. 2000: Stereospondyli. *In* Wellnhofer, P. (ed.). Handbuch der Paläoherpetologie, vol. 3B. Verlag Friedrich Pfeil, München: pp. 1–203.
Schoch, R. R. & Witzmann, F. 2011. Bystrow's Paradox: gills, fossils, and the fish-to-tetrapod transition. – Acta Zoologica (Stockholm) 92: 251–265.
Schoch, R. R. & Witzmann, F. 2012. Cranial morphology of the plagiosaurid *Gerrothorax pulcherrimus* as an extreme example of evolutionary stasis. – Lethaia 45: 371–385.
Schultze, H.-P. 1966. Morphologische und histologische Untersuchungen an Schuppen mesozoischer Actinopterygier (Übergang von Ganoid- zu Rundschuppen). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 126: 232–314.
Schultze, H.-P. 1977. Ausgangsform und Entwicklung der rhombischen Schuppen der Osteichthyes (Pisces). – Paläontologische Zeitschrift 51: 152–168.
Schultze, H.-P. & Arsenault, M. 1985. The panderichthyid fish *Elpistostege*: a close relative of tetrapods? – Palaeontology 28: 293–309.
Schwarz-Wings, D., Frey, E. & Martin, T. 2009. Reconstruction of the bracing system of the trunk and tail in hyposaurine dyrosaurids (Crocodylomorpha; Mesoeucrocodylia). – Journal of Vertebrate Paleontology

29: 453–472.
Sewertzoff, A. N. 1924. Die Entwicklung der Kiemen und Kiemengefässe bei Fischen. – Zeitschrift für wissenschaftliche Zoologie 121: 494–556.
Shishkin, M. A. 1987. The Evolution of Ancient Amphibians. Nauka, Moscow [in Russian].
Shubin, N. H., Daeschler, E. B. & Jenkins, F. A. 2006. The pectoral fin of *Tiktaalik rosae* and the origin of the tetrapod limb. – Nature 440: 764–771.
Sigurdsen, T. & Bolt, J. R. 2010. The Lower Permian amphibamid *Doleserpeton* (Temnospondyli: Dissorophoidea), the interrelationships of amphibamids, and the origin of modern amphibians. – Journal of Vertebrate Paleontology 30: 1360–1377.
Sire, J.-Y. 1985. Fibers d'ancrage et couche limitante externe á la surface des écailles du Cichlidae *Hemichromis bimaculatus* (Teleosteen, Perciforme): données ultrastructurales. – Annales des Sciences Naturelles, Zoologie, 13e série, 7: 163–180.
Sire, J.-Y. 1986. Ontogenic development of surface ornamentation in the scales of *Hemichromis bimaculatus* (Cichlidae). – Journal of Fish Biology 28: 713–724.
Sire, J.-Y. & Huysseune, A. 2003. Formation of dermal skeletal and dental tissues in fish: a comparative and evolutionary approach. – Biological Reviews 78: 219–249.
Sire, J.-Y., Donoghue, P. C. J. & Vickaryous, M. K. 2009. Origin and evolution of the integumentary skeleton in non-tetrapod vertebrates. – Journal of Anatomy 214: 409–440.
Skutschas, P. P. & Gubin, Y. M. 2012. A new salamander from the late Paleocene–early Eocene of Ukraine. – Acta Palaeontologica Polonica 57: 135–148.
Smithson, T. M. 2000. Anthracosaurs. *In* Heatwole, H. & Carroll, R. L. (eds). Amphibian biology, vol. 4: Palaeontology. Surrey Beatty & Sons, Chipping Norton: pp. 1053–1063.
Smithson, T. M., Wood, S. P., Marshall, J. E. A. & Clack, J. A. 2012. Earliest Carboniferous tetrapod and arthropod faunas from Scotland populate Romer's Gap. – Proceedings of the National Acadademy of Science 109: 4532–4537.
Stadtmüller, F. 1936. Kranium und Visceralskelett der Stegocephalen und Amphibien. *In* Bolk, L., Göppert, E., Kallius, E. & Lubosch, W. (eds). Handbuch der vergleichenden Anatomie der Wirbeltiere, vol. 4. Urban & Schwarzenberg, Berlin: pp. 501–698.
Sulej, T. & Majer, D. 2005. The temnospondyl amphibian *Cyclotosaurus* from the Upper Triassic of Poland. – Palaeontology 48: 157–170.
Taylor, M. A. 1987. How tetrapods feed in water: A functional analysis by paradigm. – Zoological Journal of the Linnean Society 91: 171–195.
Ultsch, G. R. 2012. Metabolism, gas exchange, and acid–base balance of giant salamanders. – Biological Reviews 87: 383 – 601.
Vickaryous, M. K. & Hall, B. K. 2006. Osteoderm morphology and development in the Nine-Banded Armadillo, Dasyceps novemcinctus (Mammalia, Xenarthra, Cingulata). – Journal of Morphology 267: 1273–1283.
Vickaryous, M. K. & Hall, B. K. 2008. Development of the dermal skeleton in *Alligator mississippiensis* (Archosauria, Crocodylia) with comments on the homology of osteoderms. – Journal of Morphology 269: 398–422.
Vorobyeva, E. I. & Schultze, H.-P. 1991. Description and systematics of panderichthyid fishes with comments on their relationship to tetrapods. *In* Schultze, H.-P. & Trueb, L. (eds). Origins of higher groups of tetrapods. Comstock Publishing Associates, Ithaca: pp. 68–109.
Wang, N.-Z., Donoghue, P. C. J., Smith, M. M. & Sansom, I. J. 2005. Histology of the galeaspid dermoskeleton and endoskeleton, and the origin and early evolution of the vertebrate cranial endoskeleton. – Journal of Vertebrate Paleontology 25: 745–756.
Wake, M. H. 1989. Metamorphosis of the hyobranchial apparatus in *Epicrionops* (Amphibia: Gymnophiona: Rhinatrematidae): replacement of bone by cartilage. – Annales des Sciences Naturelles Zoologie 10: 171–182.
Wake, D. B. & Deban, S. M. 2000. Terrestrial feeding in salamanders. *In* Schwenk, K. (ed.). Feeding: form, function and evolution in tetrapod vertebrates. Academic Press, San Diego: pp. 95–116.
Warren, D. E. & Jackson, D. C. 2005. The role of mineralized tissue in the buffering of lactic acid during anoxia and exercise in the leopard frog *Rana pipiens*. – Journal of Experimental Biology 208: 1117–1124.
Witzmann, F. 2004. The external gills of Palaeozoic amphibians. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 232: 375–401.
Witzmann, F. 2006. Cranial anatomy and ontogeny of the Permo-Carboniferous temnospondyl *Archegosaurus decheni* from the Saar-Nahe Basin, Germany. – Transactions of the Royal Society of Edinburgh, Earth Sciences 96: 131–162.
Witzmann, F. 2007. The evolution of the scalation pattern in temnospondyl amphibians. – Zoological Journal of the Linnean Society 150: 815–834.
Witzmann, F. 2009. Comparative histology of sculptured dermal bones in basal tetrapods, and the

implications for the soft tissue dermis. – Palaeodiversity 2: 233–270.

Witzmann, F. 2010. A skull fragment of a Devonian tetrapod in the collection of the Museum für Naturkunde Berlin showing a unique lateral line morphology. – Fossil Record 13: 297–302.

Witzmann, F. 2011. Morphological and histological changes of dermal scales during the fish-to-tetrapod transition. – Acta Zoologica 92: 281–302.

Witzmann, F. 2013. Phylogenetic patterns of character evolution in the hyobranchial apparatus of early tetrapods. – Transactions of the Royal Society of Edinburgh: Earth Sciences 104: 145–167.

Witzmann, F. & Schoch, R. R. 2006. Skeletal development of the temnospondyl *Acanthostomatops vorax* from the Lower Permian Döhlen basin of Saxony. – Transactions of the Royal Society of Edinburgh: Earth Sciences 96: 365–385.

Witzmann, F. & Soler-Gijón, R. 2010. The bone histology of osteoderms in temnospondyl amphibians and in the chroniosuchian *Bystrowiella*. – Acta Zoologica (Stockholm) 91: 96–114.

Witzmann, F. & Schoch, R. R. 2013. Reconstruction of cranial and hyobranchial muscles in the Triassic temnospondyl *Gerrothorax* provides evidence for akinetic suction feeding. – Journal of Morphology 274: 525–542.

Witzmann, F., Schoch, R. R. & Maisch, M. 2008. A relict basal tetrapod from Germany: first evidence of a Triassic chroniosuchian outside Russia. – Naturwissenschaften 95: 67–72.

Witzmann, F., Scholz, H., Müller, J. & Kardjilov, N. 2010. Sculpture and vascularization of dermal bones, and the implications for the physiology of basal tetrapods. – Zoological Journal of the Linnean Society 160: 302–340.

Witzmann, F., Schoch, R. R., Hilger, A. & Kardjilov, N. 2012. Braincase, palatoquadrate and ear region of the plagiosaurid *Gerrothorax pulcherrimus* from the Middle Triassic of Germany. – Palaeontology 55: 31–50.

Worthington, R. D. & Wake, D. B. 1970. Larval morphology and ontogeny of the ambystomatid salamander, *Rhyacotriton olympicus*. – The American Midland Naturalist 85: 349–365.

Yates, A. M. & Warren, A. A. 2000. The phylogeny of the "higher" temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. – Zoological Journal of the Linnean Society 128: 77–121.

Zylberberg, L. & Castanet, J. 1985. New data on the structure and the growth of the osteoderms in the reptile *Anguis fragilis* L. (Anguidae, Squamata). – Journal of Morphology 186: 327–342.

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Appendices

Dermal bone sculpture in early tetrapods: external morphology, histology and possible functions

Appendix 1

Witzmann, F., Scholz, H., Müller, J. & Kardjilov, N. 2010. Sculpture and vascularization of dermal bones, and the implications for the physiology of basal tetrapods. – Zoological Journal of the Linnean Society 160: 302–340.

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Sculpture and vascularization of dermal bones, and the implications for the physiology of basal tetrapods

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Sculpture of dermal bones and their vascularization in basal tetrapods are closely connected. Ontogenetic data suggest that the large vessels that coursed to the superficial bone surface induced the formation of sculptural ridges and tubercles around their openings. Imprints show that the vessels continued on the bone surface and coursed within furrows or pits, where they were protected by the sculpture from mechanical damage. Dermal bone histology indicates a consolidation of the integument in basal tetrapods by strong, mineralized Sharpey's fibres in the sculptural ridges and tubercles, and by the presence of metaplastic tissue in several taxa. Because of the tight integration of bone and dermis, the large vessels were not able to spread over the sculptural elements, but instead had to pass interosseously. The diverse sculptural morphologies depend on the variation in height and width of the 'nodal points' and their connecting ridges, and in the size and shape of the enclosed cells and furrows. A principal component analysis (PCA) and discriminant function analysis (DFA) of 47 basal tetrapod taxa with 12 discrete characters shows that dermal sculpture is suited for distinguishing some main basal tetrapod lineages. Taxa that are interpreted as being largely aquatic have generally a more regular sculpture than presumably terrestrial ones.

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ADDITIONAL KEYWORDS: fish–tetrapod transition – integument – Mesozoic – Palaeozoic – Temnospondyli – vessels.

The dermal bone sculpture (or ornament) of basal tetrapods, and its functional implications, remains one of the unresolved enigmas in vertebrate palaeontology. Most of the Palaeozoic and Mesozoic stem tetrapods, temnospondyls, stem amniotes, and basal amniotes have dermal bones that are conspicuously sculptured by tubercles, pits, ridges, and furrows. This applies to the dermal skull roof, the mandible, the dermal pectoral girdle (interclavicle and clavicles), and, if present, the osteoderms of the trunk and gular region. Only those parts of the superficial bone surface that are directly overlain by the integument are sculptured, whereas the deep surface of the bones or sites of attachment for ligaments and muscles are unsculptured.

Although dermal sculpture was recognized early as characteristic for basal tetrapods (e.g. von Meyer, 1858; Fraas, 1889; Fritsch, 1889; Zittel, 1911), it was Bystrow (1935) who provided the first comprehensive description of dermal sculpture and its morphogenesis. He distinguished between a polygonal sculpture of pits and ridges, which is first formed ontogenetically in the ossification centre of each bone, and the radially aligned ridges and furrows in the bone periphery, which reflect the direction of bone growth. By comparing the orientation and extent of

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these ridges in the particular bones, Bystrow (1935) was able to detect the relative growth rate of different skull regions. He also demonstrated openings of large vascular canals within the furrows and pits, as well as numerous small pores that may be distributed all over the bone surface. The small pores were interpreted by him as being part of a capillary network within the bone (the rete vasculosum) that originally belonged to the dermis, and was later enclosed by bone during its appositional growth (Bystrow, 1935, 1947). Bystrow (1947) hypothesized that the network served for cutaneous respiration, and distinguished between primarily aquatic basal tetrapods ('hydrophilous labyrinthodonts') that possessed the vascular network, and relied to a large degree on cutaneous respiration, and rather terrestrial forms ('xerophilous labyrinthodonts'), in which this network was absent, and which breathed mainly via their lungs. The absence of the vascular network in the aquatic *Dvinosaurus* was explained by the fact that this neotenic temnospondyl retained gill breathing throughout its lifetime, which rendered gas exchange via the skin unnecessary (Bystrow, 1947).

In 1974, Coldiron showed that the collagen fibres of the bone are arranged parallel with one another in the deep cortex and in the middle, spongy region of the bone, but are non-parallel and randomly oriented in the sculptured superficial cortex of *Eryops* and *Alligator*. Thus, Coldiron (1974) concluded that dermal bone sculpture in basal tetrapods and crocodilians is a strengthening adaptation, by distributing the stress that acted on the dermal skull roof, especially during feeding. He did not accept Bystrow's (1947) suggestion about the involvement of the rete vasculosum in cutaneous respiration, as the capillaries describe an irregular pathway, and thus an inefficient route of the blood to the bone surface and the skin.

After the work of Bystrow and Coldiron, no studies dealt exclusively with the morphology and functional aspects of dermal bone sculpture in temnospondyls and other basal tetrapods. However, the alteration of the sculptural pattern during ontogeny has been used in attempts to determine a kind of metamorphosis in basal tetrapods. Already Credner (1886) and Bystrow (1935) suggested that the development of the polygonal sculpture marks the time of metamorphosis in temnospondyls from the larval to the juvenile phase. Developing this approach, Boy (1978, 1988, 1990, 1993) and Boy & Sues (2000) elaborated a model to distinguish different growth phases in selected temnospondyls on the basis of the outer morphology of dermal sculpture.

Seibert, Lillywhite & Wassersug (1974) demonstrated experimentally that water loss by evaporation is significantly reduced in one hylid and one pelobatid species with integumentary–cranial co-ossification in the skull, as compared with two ranid and two hylid species in which co-ossification is absent. These authors similarly considered dermal bone sculpture in basal tetrapods as co-ossification with the integument, and suspected that it reduced water loss via the skin in terrestrial forms.

In their work on the rhytidosteid temnospondyl *Pneumatostega*, Cosgriff & Zawiskie (1979) suggested that the tubercular sculpture of the dermal bones was reflected in the overlying integument, and thus increased its surface area. Like Bystrow (1947), these authors concluded that together with the extensive vascularization of the superficial bone surface, dermal sculpture was an adaptation for cutaneous respiration. Schoch (2001) accepted Cosgriff & Zawiskie's (1979) hypothesis for the temnospondyl *Sclerocephalus*. He further pointed out that among temnospondyls, the primarily aquatic stereospondyls have a more regular sculptural pattern of cells and furrows, whereas the sculpture is quite irregular in the more terrestrial temnospondyls. He interpreted the sculptural ridges and furrows as a sort of mechanical protection of the soft tissue dermis, including vessels and nerves when the animals were shedding the superficial parts of the skin. However, a large-scale investigation concerning a possible correlation between sculptural pattern and presumed mode of life has not been carried out so far. This might also result from the fact that the mode of life is often difficult to assess, and is thus controversially discussed in certain basal tetrapods (see below).

Dias & Richter (2002), in their paper on the dermal scales of the temnospondyl *Australerpeton*, also addressed the issue of the possible function of dermal sculpture of temnospondyl dermal bones. They considered this phenomenon as either a strengthening adaptation of the bones or as a tight anchorage of the overlying skin.

Studying thin sections of basal tetrapod osteoderms, Witzmann & Soler-Gijón (2008) found strong bundles of mineralized Sharpey's fibres penetrating the sculptural ridges and tubercles, whereas the fibres are scarce or absent in the sculptural furrows. These authors therefore concluded that the overlying integument must have been tightly attached to the dermal sculpture.

In this paper, the outer sculptural morphology is investigated in a wide variety of basal tetrapods, from the finned stem tetrapod *Panderichthys* to basal amniotes. First, a morphological and morphogenetic approach is followed. Sculptural patterns are distinguished, and the evolution and development of these sculptural patterns is described. Also, the correlation between the position of the numerous openings of the vascular canals and of the bone sculpture is studied.

Second, the phylogenetic signal of sculptural pattern is ascertained. For this, a principal component analysis (PCA) and discriminant function analysis (DFA), based on 12 discrete characters of dermal sculpture, is performed. In this connection, we will investigate whether there is a correlation between the sculptural pattern and the presumed mode of life, i.e. primarily aquatic or terrestrial. Finally, the possible functions of dermal sculpture are discussed. This study contains the investigation of thin sections of sculptured dermal bones of selected basal tetrapods, but a detailed description of bone histology of the dermal skull and pectoral girdle in a wide array of basal tetrapod taxa will be published elsewhere (Witzmann, in press).

ANATOMICAL TERMS AND PHYLOGENETIC FRAMEWORK

The following terms are used to describe dermal bone sculpture and dermal bones (see Fig. 1A, B): in the polygonal sculpture, each rounded or rather hexagonal 'cell' is formed by sculptural ridges that enclose a superficially concave area: the 'pit' (Fig. 1A). Each cell contains at least one 'vascular opening' (i.e. the opening of a large vascular canal) at its bottom. The points of intersection in which the sculptural ridges meet are designated here as 'nodal points'. They might be pronounced in height and width with respect to the ridges, and are then designated as 'tubercular nodal points' or just 'tubercles'. When the sculptural ridges are suppressed with respect to the nodal points, the sculpture is termed 'tubercular' (Fig. 1B). In the radial sculpture, the radially aligned sculptural ridges delimit 'sculptural furrows' (Fig. 1A). Vascular openings in the sculptural furrows are often accompanied proximally by a sculptural ridge, the 'axilla ridge'. 'Pores' are tiny openings that may or may not be present on the superficial surface, and belong to capillaries within the bone. The term 'superficial surface' refers to the sculptured surface of the dermal bone that faces the body surface, whereas the deep surface is oriented to the visceral surface of the body. The term 'interior' corresponds to the middle or central part of a dermal bone (*sensu* Scheyer & Sánchez-Villagra, 2007). In general, the dermal bones show a diploë structure, i.e. a cancellous or trabecular middle region is mantled by compact superficial and deep cortices.

In the present study, the analyses of Ruta, Coates & Quicke (2003) and Ruta & Coates (2007) are taken as the phylogenetic framework of basal tetrapod interrelationships, and the intrarelationship of temnospondyls is based on the analyses by Schoch & Milner (2000) and Yates & Warren (2000). According to Ruta *et al.* (2003) and Ruta & Coates (2007), embolomeres, seymouriamorphs, and lepospondyls are stem amniotes, whereas the monophyletic lissamphibia are nested within the temnospondyls. In contrast, the phylogenetic analysis of Vallin & Laurin (2004) supports a monophyletic lissamphibia derived from lepospondyls, and temnospondyls, embolomeres, and seymouriamorphs belong to stem-group tetrapods. More recently, the phylogenetic analysis of Anderson *et al.* (2008) found lissamphibians to be polyphyletic, with frogs and salamanders nested within temnospondyls, whereas caecilians are derived from lepospondyls.

The term 'crown-group tetrapod' is used here in the sense of Hennig (1966) as encompassing the last common ancestor of all living tetrapods and all of its descendants, both extinct and extant. The stem-group tetrapods define all fossil taxa that are more closely related to crown-group tetrapods than to the extant group that is the closest relative of the crown-group tetrapods [either actinistians (e.g. Zhu & Schultze, 2001) or dipnoans (e.g. Cloutier & Ahlberg, 1996)].

MATERIAL AND METHODS

The investigated basal tetrapod taxa and their inventory numbers are listed in Appendix 1. The outer bone sculpture was investigated using a binocular microscope, and, in the case of small-growing forms, the bone surface was studied by SEM. For thin sectioning, the dermal bone fragments were fist embedded in synthetic resin (Paraloid B72, an ethyl-methacrylat copolymer), and were then cut vertically, either parallel or transverse with the direction of the sculptural ridges. The slides were prepared with a thickness of approximately 40–60 μm using the standard method of Chinsamy & Raath (1992), and were examined using a Leica DC 300 polarizing stereosmicroscope, with transmitted ordinary and polarized light.

For the demonstration of the large vascular canals within the bones, neutron tomography has been applied. This method enables investigations of the macroscopic internal structures of large samples (up to hundreds of cubic centimetres) with a spatial resolution of up to 50 μm. The neutron beam can pass through centimetres of metal, but it is easily attenuated by small quantities of light elements like hydrogen, boron, and lithium. The neutron tomography (NT) instrument CONRAD (Cold Neutron RADiography) at Helmholtz Zentrum Berlin (HZB) is located at the end of the curved neutron guide NG1b facing the cold source of the BER-II reactor. The facility uses point-source geometry in order to increase the image resolution. For this purpose, an additional collimation system, consisting of a flight tube of 5 m in length and a set of diaphragms, is installed.

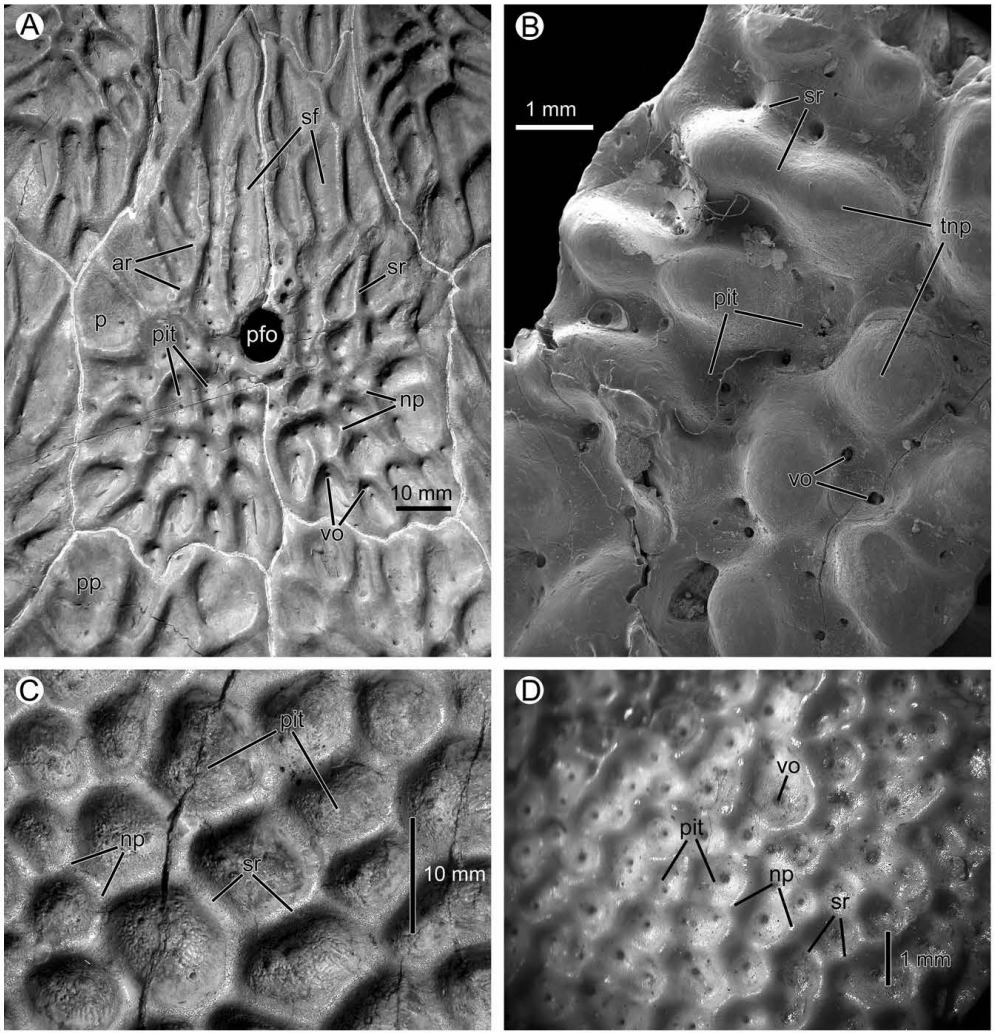


Figure 1. A, *Mastodonsaurus giganteus* (Stereospondyli, Capitosauroidea), SMNS without number. Parietals showing polygonal sculpture in the ossification centre and radial sculpture in the periphery. B, *Gerrothorax pustuloglomeratus* (Stereospondyli, Plagiosauridae), SMNS without number. SEM photograph of dorsal osteoderm showing tubercular sculpture. C, *Metoposaurus fraasi* (Stereospondyli, Trematosauroidea), UCMP 27103. Close-up of the regular polygonal sculpture on the parietal. D, *Wetlugasaurus samarensis* (Stereospondyli, Trematosauroidea), PIN 4627/1. Close-up of polygonal sculpture on the parietal; the nodal points are elevated with respect to the sculptural ridges. For abbreviations, see text.

The NT experiments were performed at the CONRAD facility. The neutron guide provides a cold neutron flux at the sample position of approximately 10^7 neutrons cm^{-2} s^{-1}. The available beam size at the sample position is 10×10 cm^2. The detector system is based on a 16-bit Peltier-cooled CCD camera (Andor DW436N-BV) with a 2048×2048-pixel target sensor. The images obtained from the LiZnS scintillator are projected via a mirror and a lens system onto the CCD chip. The 3D tomography was obtained from 300 radiographs at different projections, covering 180° (0.6° per projection). The estimated geometrical resolution was about 200 µm per pixel. For the tomographic reconstruction, a mathematical algorithm (filtered back projections) was used.

A PCA and a discriminant function analysis (DFA) of 47 taxa of basal tetrapods studied herein, and their sculptural morphology, was processed using PAST 1.82b (Hammer, Harper & Ryan, 2001) in order to explore the morphospace occupation of the taxa, and to study the relationship of all taxa in context. The two questions for this analysis were: (1) whether the phylogenetic relationships of the taxa are reflected by the morphospace occupation, and (2) whether the mode of life (i.e. aquatic or terrestrial) is reflected by the morphospace occupation. A set of 12 discrete characters concerning the morphology of the dermal sculpture was defined for this study, resulting from first-hand examination of dermal bone sculpture on the basal tetrapod skulls. The character states were classified on a nominal scale (see Appendix 2 for the description of the characters, and Appendix 3 for the coded character states). The characters refer only to the bones of the postorbital skull table (parietals, postparietals, and the temporal series), because the sculpture on the squamosal is predominantly radially aligned and shows few differences between the taxa, and the pattern on the premaxilla, maxilla, nasal, frontal, and quadratojugal is rather irregular. Furthermore, only adult or presumably adult skulls have been considered. The state order does not reflect polarity.

Tests for a phylogenetic signal in the dermal sculpture characters were performed using the software package Mesquite 2.6 (Maddison & Maddison, 2009). The terminal taxa were reshuffled 10 000 times, and each character was optimized onto the resulting topologies. The original number of steps of each character was then compared against the 0.05 threshold, in order to test if there are significantly fewer steps than in 95% of the remaining trees, which would indicate the presence of a phylogenetic signal.

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York, USA; CMNH, Cleveland Museum of Natural History, Cleveland, OH, USA; LFUG, Landesamt fur Umwelt und Geologie, Freiberg in Sachsen, Germany; MB, Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin, Germany; MCZ, Museum of Comparative Zoology, Harvard, Cambridge/Mass., USA; MGUH, Geological Museum, University of Copenhagen, Denmark (stored temporarily in the Museum of Comparative Zoology, Cambridge, UK); PIN, Palaeontological Institute of the Russian Academy of Sciences, Moscow, Russia; ROM, Royal Ontario Museum, Toronto, ON, Canada; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UCMP, University of California, Museum of Paleontology, Berkeley, USA; UMZC University Museum of Zoology, Cambridge, England, UK.

ANATOMICAL ABBREVIATIONS

ang, angular; ar, axilla ridge; d, dentary; eo, exoccipital; fnp, future nodal point; GM, growth marks; lls, lateral line sulcus; np, nodal point; oc, oblique large vascular canal; orb, orbit; p, parietal; PFB, parallel-fibred bone; pfo, parietal foramen; pp, postparietal; PVC, primary vascular canal; sf, sculptural furrow; ShF, Sharpey's fibres; SO, secondary osteon; sq, squamosal; sr, sculptural ridge; sr-sc, sculptural ridge of smaller cell; t, tabular; tnp, tubercular nodal point; vc, vertical large vascular canal; vi, imprint of vessel; vo, vascular opening.

GENERAL MORPHOLOGY AND DEVELOPMENT

NODAL POINTS AS HOMOLOGOUS SCULPTURAL POINTS OR 'LANDMARKS'

In basal tetrapods, two basic dermal sculptural patterns can generally be distinguished: the polygonal and the radial patterns (Figs 1, 2), whereas transitions between the two different patterns exist. The tubercular pattern is a special case, and can be derived from these two patterns (see below). The polygonal sculpture is taken as the starting point for the description of the different sculptural patterns and their development.

Polygonal sculpture

As outlined above, the polygonal sculpture consists of rounded or hexagonal cells, and each cell consists of a pit enclosed by sculptural ridges. Each pit contains at least one vascular opening at its bottom (Fig. 1). Because the points of intersection of sculptural ridges, the nodal points, are visible in both basic sculptural patterns, they are interpreted here as homologous points that allow comparison between the

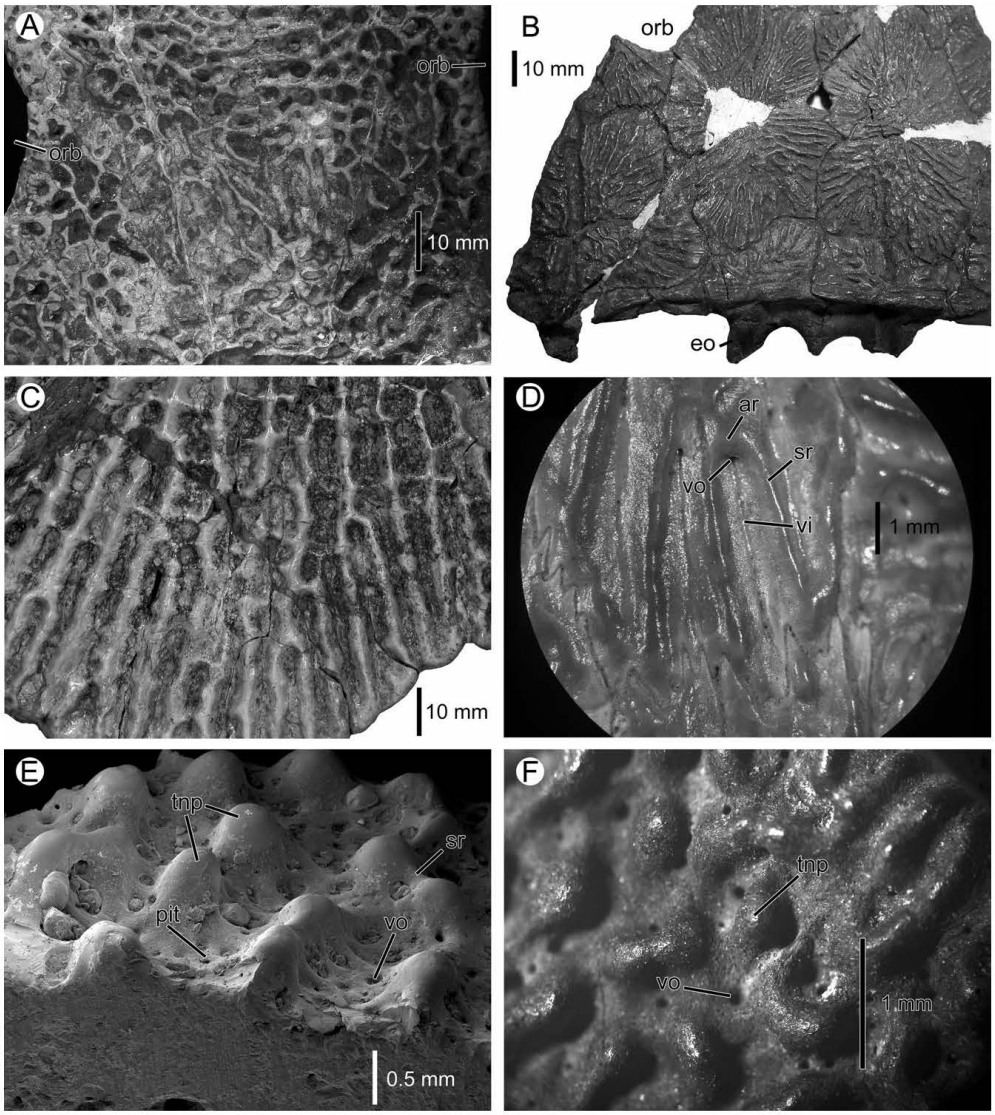


Figure 2. A, *Eryops megacephalus* (Temnospondyli, Eryopidae), MCZ 3233, cast. Irregular polygonal sculpture in the interorbital region. B, *Dvinosaurus primus* (Temnospondyli, Dvinosauria), PIN 156/10. Posterior part of skull table with radial sculpture. C, *Metoposaurus fraasi* (Stereospondyli, Trematosauroidea), UCMP 27103. Posterior portion of interclavicle with radial sculpture. D, *Thoosuchus jakovlevi* (Stereospondyli, Trematosauroidea), SMNS 80064. Close-up of the radial sculpture on the postfrontal, with imprints of vessels within the sculptural furrows. E, *Panderichthys rhombolepis* (stem tetrapod, Elpistostegalia), MB.f.17548. SEM photograph of tubercular sculpture of dermal bone of the skull or pectoral region. F, *Chroniosaurus dongusensis* (Chroniosuchia, Chroniosuchidae), PIN 3713/38. Close-up of tubercular sculpture on the parietal. For abbreviations, see text.

different patterns. There is much variation between taxa concerning the height and width of the nodal points with respect to the sculptural ridges. For example, in the skull table of *Metoposaurus fraasi* Lucas, 1904 (Fig. 1C), the nodal points and ridges approximately correspond in height, which gives this sculpture a rather regular appearance. In contrast, *Wetlugasaurus* has nodal points that are slightly raised with respect to the sculptural ridges (Fig. 1D). In *Eryops*, the cells are more variable in size and shape, the sculptural ridges differ in height and width, and the nodal points are often accentuated and higher than the ridges (Fig. 2A).

Radial sculpture

Some basal tetrapods possess a primarily radially arranged sculpture. This pattern is composed of sculptural ridges and furrows that radiate outwards from the ossification centre of each bone, as visible for example in the temnospondyl *Dvinosaurus* (Fig. 2B). Further examples of radial sculpture are the peripheral areas of temnospondyl interclavicles (Fig. 2C) and of the dermal skull bones of the temnopsondyl *Thoosuchus* (Fig. 2D). The radial sculpture is basically a larval or juvenile character, and as Bystrow (1935) demonstrated, the polygonal sculptural pattern develops ontogenetically from the radial pattern by the formation of dividing walls within the sculptural furrows (see below). Nevertheless, as the example *Thoosuchus* shows, this pattern may also be retained in adult specimens.

Tubercular sculpture

In certain taxa, the sculptural ridges are low or subdued, and the nodal points are well developed. Then, the sculptural pattern appears to be 'tubercular'. This is the case, for example, in the Devonian stem tetrapods *Panderichthys* (Fig. 2E) and *Ichthyostega*, in temnospondyls like the plagiosaurid *Gerrothorax* (Fig. 1B) and the dissorophoid *Micropholis*, or in chroniosuchians like *Chroniosaurus* (Fig. 2F). In spite of the suppression of the sculptural ridges in these forms, the pits (in a basically polygonal sculpture) and furrows (in areas with a basically radial sculpture) are readily visible as concave areas that contain one or more vascular openings on the bottom. When several nodal points are connected via high ridges, the sculpture may appear vermiculate. In some basal tetrapods with tubercular sculpture, the nodal points are grown out to distinct projections or protuberances of irregular size, as seen among temnospondyls like the plagiosaurid *Plagiosuchus*. In this taxon, moderately high ridges enclose small, rounded pits in the ossification centres of the bones. The nodal points are much pronounced in width and height, and are often larger than the pits themselves. Similarly pronounced nodal points are also visible in the dissorophids *Platyhystrix* and *Kamacops*. In the dissorophid *Iratusaurus*, they form a median sagittal crest on the posterior part of the skull table. The tubercular sculpture of *Gerrothorax pulcherrimus* (Fraas, 1913) follows a basically radial pattern. Pronounced tubercles are aligned on radial, low ridges, and thus appear arranged in rows, similar to the bones of the skull table in *Chroniosaurus* (see below).

'Aberrant sculpture'

Some basal tetrapods possess a peculiar sculpture with knobs and spines, which has sometimes been called 'aberrant'. However, these conspicuous features can also be traced back to the patterns described above. As examples, the zatracheid temnospondyls and the lanthanosuchid parareptiles are mentioned in this paragraph. In the zatracheid *Zatrachys*, small areas of rounded polygonal cells with tubercular nodal points are developed in small areas that represent the ossification centres, from which ridges and furrows extend radially outwards (Fig. 3A). This radial pattern is often subdued on a concave surface, especially on the jugal, the cheek, and the snout between pronounced crests, so that the surface sculpture appears indistinct in these regions. In contrast, the zatracheid *Acanthostomatops* bears a 'more normal' sculpture, of irregular cells and radial ridges with tubercular nodal points. The dermal skull bones of the lanthanosuchid *Lanthanosuchus* have a very strong sculpture of rounded cells of variable shape and size (Fig. 3B). The height and width of the dorsally rounded ridges differ conspicuously, and some are very pronounced. Prominent ridges can enclose several smaller cells with lower and thinner ridges. Many nodal points are distinctly accentuated, and form tubercles or protuberances. In the other known lanthanosuchid, *Lanthaniscus*, the sculptural pattern consists basically of radially oriented ridges. Small areas with rounded hexagonal cells are present in the ossification centres of the bones. The ridges vary conspicuously in height and width. They are broadly rounded dorsally, and the nodal points are frequently pronounced and form distinct, partially fused tubercles. In its general appearance, the tubercular, radiating sculpture is reminiscent to that of *Zatrachys* (Fig. 3A).

VARIABLE SCULPTURAL PATTERNS IN DIFFERENT REGIONS OF THE SKULL ROOF

As pointed out by Bystrow (1935), the bones of the skull that show positive allometric growth possess a greater area of radial sculpture compared with the slower-growing parts of the skull. In general, positive allometry can be observed in the preorbital region

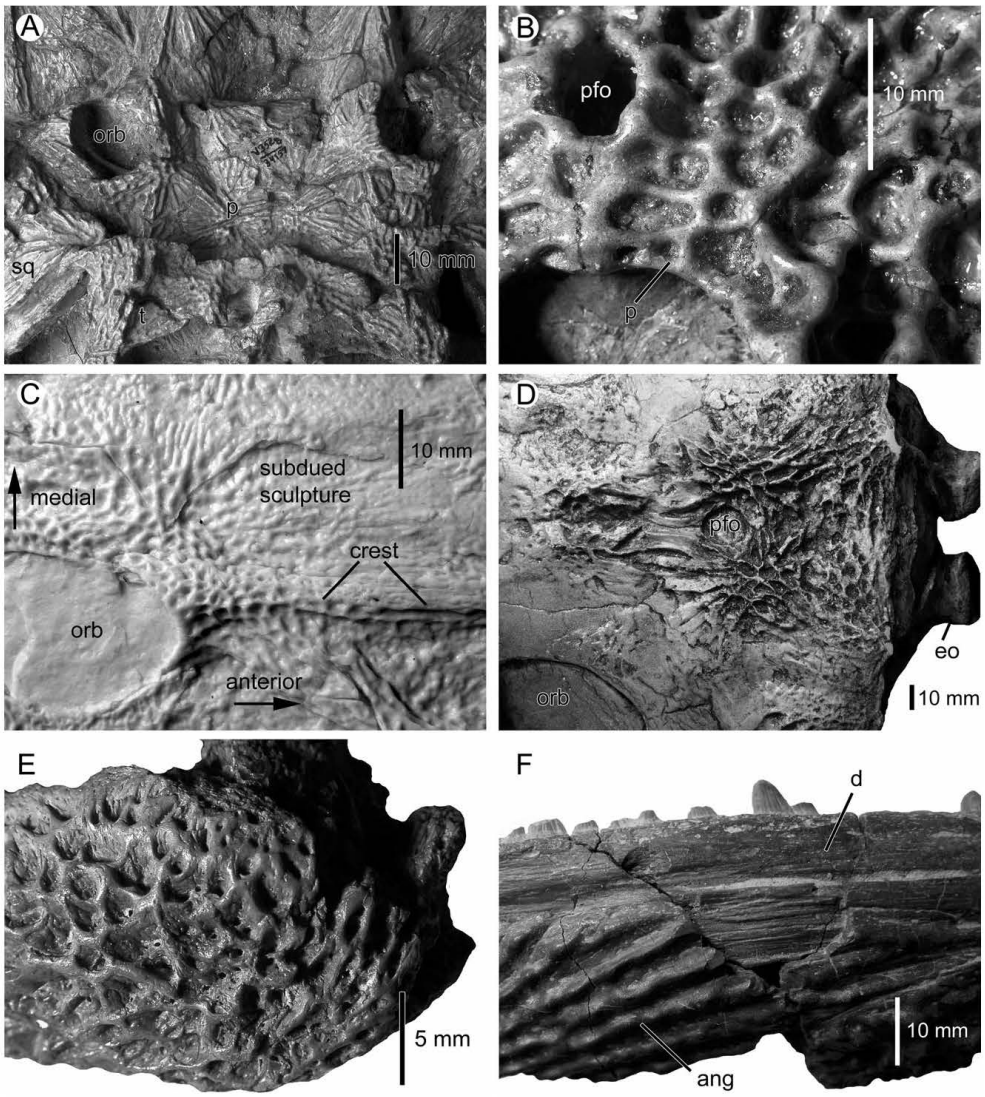


Figure 3. A, *Zatrachys serratus* (Temnospondyli, Zatracheidae), UCMP 34137. Posterior portion of the skull with radial and polygonal/tubercular sculpture. B, *Lanthanosuchus watsoni* (Parareptilia, Lanthanosuchidae), PIN 271/1. Posterior skull table with pronounced sculpture. C, *Cochleosaurus bohemicus* (Temnospondyli, Edopoidea), MB.Am.80, cast. The dermal sculpture is much subdued medial to the crest extending from the orbit to the snout. D, *Vigilius wellesi* (Stereospondyli, Brachyopoidea), ROM 23857, cast. Posterior portion of the skull, with sculptured bones (median part of the skull table) and bones that are largely smooth. E, *Melosaurus uralensis* (Stereospondylomorpha, Melosauridae), PIN 161/3. Symphysis in ventrolateral view. F, *Gerrothorax pustuloglomeratus* (Stereospondyli, Plagiosauridae), SMNS without number. Part of the mandible in labial view: whereas the angular is heavily sculptured, the dentary is only faintly striated. For abbreviations, see text.

(especially the nasal, prefrontal, lacrimal, and anterior part of the frontal) as well as in the cheek (especially the squamosal) (Bystrow, 1935; Witzmann & Scholz, 2007). As compared with the skull table, the sculpture on the preorbital bones appears generally more irregular, as the cells in the ossification centres and the radiating furrows often differ in shape and size, and there is also much variation in height and width of the sculptural ridges. Furthermore, the nodal points are frequently more pronounced with respect to the ridges.

Apart from these differences, the cells are smaller, and thus have a higher density on the lateral parts of the premaxilla and the anterior part of the maxilla compared with other parts of the skull in many basal tetrapods. Here, the cells resemble narrow funnels, and their ridges are thinner and are often sharply edged superficially. Closer to the jaw margin, the cells are directed ventrally (towards the mouth opening), and the region immediately next to the jaw margin often has a rather smooth surface. Smaller and deeper cells also occur in those areas of the skull roof that are raised and dorsally convex. In *Eryops*, *Edops*, and *Cochleosaurus* (Fig. 3C), for example, this is visible anterior to the orbits (mostly in the region of the prefrontals), posterior to the orbits (on a crest between orbit and tabular), and medially adjacent to the nares.

In contrast to these exposed parts of the skull roof, the superficially concave areas (e.g. the interorbital region) often bear an irregular, more poorly-defined sculptural pattern, with low sculptural ridges and nodal points. In *Cochleosaurus*, for instance, the raised crests that extend from the anterior part of the snout to the orbits, and the crests that extend from the orbits to the lateral margin of the snout (Sequeira, 2004), bear a sculpture of small cells with thin sculptural ridges. Between these crests, the surface bears a much suppressed, irregular polygonal sculpture, with indistinct, low radial ridges in the periphery (Fig. 3C). A similar situation is present in the radial pattern of *Zatrachys* (see above). In the brachyopid temnospondyl *Vigilius*, only the median portion of the skull table, i.e. parietals and postparietals, the posterior part of the frontals, and the centres of the squamosals, are sculptured, with distinct ridges around pits and furrows (Fig. 3D). The supratemporals and the centres of the postfrontals bear an irregular sculpture of lower ridges, whereas the remaining dermal skull bones possess a largely smooth surface. The strongly sculptured regions of the skull roof are upraised (exposed) with respect to the less sculptured and smooth regions. A very similar pattern occurs on the dermal skull roof of the plagiosaurid *Plagiosuchus*, in which the sculptured parts are distinctly exposed relative to the smooth parts of the bones. In the plagiosaurid *Plagiosternum*, the sculpture is most regular and pronounced on the parietal portion posterior to the parietal foramen, and this region is elevated compared with the remaining skull table.

Sculpture of the lower jaw

A high density of small sculptural pits can be found in the symphysis of many basal tetrapods, similar to the sculpture on the lateral parts of the premaxilla and maxilla. The cells and the associated vascular openings are directed posterodorsally and dorsally towards the jaw margin (Fig. 3E), a pattern that is symmetrical with the cells of the premaxilla and of the anterior part of the maxilla (see above). As in the upper jaw, the part of the symphysis close to the jaw margin often has a subdued sculpture [e.g. visible in the temnospondyls *Trimerorhachis*, *Mastodonsaurus*, and *Gerrothorax* (Fig. 3F), the colosteid *Greererpeton*, and the baphetid *Megalocephalus*].

Apart from the symphysis, the dentary most often possesses a sculpture of weakly developed, low longitudinal ridges and furrows, and the vascular openings are directed posteriorly. Like the symphysis, the dorsalmost part of the dentary often has a subdued sculpture of faint longitudinal striae. The dentary of a very large mandible of *Edops* (MCZ 1378) bears a polygonal sculptural pattern that extends almost to the dorsal edge of the bone.

Unlike the dentary, the splenials usually have a distinct polygonal sculpture on their lateral and ventral surface, whereas the lingual portion is rather smooth. A similar pattern applies to the angular, especially to the angle of the jaw. Here, most often, radially aligned ridges and furrows extend dorsally and anteriorly from the cells in the ossification centre.

Dermal sculpture and vascularization

Large canals and vascular openings

As already observed by Bystrow (1935), large canals run through the middle region of the bone, and reach the superficial surface through vascular openings. In the ossification centre, or in other areas where the dermal sculpture is composed of cells, the canals extend roughly vertically or at a steep angle to the superficial surface of the bone (Fig. 4A, B). Their vascular openings are located on the bottom of a pit, and are thus completely surrounded by ridges (e.g. Figs 1A, D, 4A). When more than one vascular opening is present on the bottom of a pit, the openings are sometimes separated from each other by low sculptural ridges of a second order within the pit (Fig. 4C). In the more peripheral parts of each dermal bone, where the sculptural ridges and furrows are

aligned radially, the large canals open obliquely towards the bone surface, towards the periphery of the bone (Fig. 4A, B, D). Where this happens, the bone has formed a sculptural ridge proximal to the vascular opening ('in its back'). This ridge is referred to here as the 'axilla ridge' of the vascular opening (Figs 1A, 4E, F). The axilla ridge continues laterally in two proximo-distally (i.e. radially)-directed sculptural ridges. The course of the large vessels on the bone surface is frequently preserved as an imprint within the sculptural furrows (Figs 2D, 5). The imprints of large vessels are always restricted to the bottom of the furrows and pits, and they never extend on top of the sculptural ridges or tubercles. In some cases, imprints show that two large vessels left the same vascular opening. The imprints further demonstrate that the vessels branched into several smaller ones (Fig. 5), which presumably led to anastomosing capillaries. The vessels always follow the morphological furrows on the bone surface between ridges and/or tubercles. Whereas the large vessels are rather long on the bone surface within the sculptural furrows, they were quite short within the sculptural cells, and ramified into capillaries soon after they left the vertical canals. This is indicated by the imprints of the capillaries on the lateral walls of the sculptural cells (e.g. in *Plagiosuchus*).

These observations show that the dermal sculpture is closely connected with the vascular canals of the bone. There is no cell and no sculptural furrow without at least one canal that opens into it via a vascular opening on its bottom. Apart from their increase in thickness, the dermal bones grew radially; therefore, the large vessels within the bone had to be arranged in a radial direction to supply the growing parts of the bone, and to connect with large canals of the adjacent bones. The orientation of the sculptural ridges and furrows reflects the orientation of the vessels within the bone and on its surface, and, as already stressed by Bystrow (1935), the direction of growth of the bones. Once a large vessel had left a vascular opening and continued in a sculptural furrow, it was 'accompanied' on its sides by sculptural ridges, or was surrounded by ridges, as in a funnel, when it opened into a cell.

The capillaries (rete vasculosum)

Fritsch (1889: fig. 129) illustrated the parietal of a *Cochleosaurus* specimen that bears several tiny pores on its sculptural ridges, designated by him as *nährporen* (nutrient pores). In contrast to the 'vascular openings', which are restricted to the concave areas, Bystrow (1935) found pores corresponding to Fritsch's *nährporen* both on the ridges and in the pits and furrows of the stereospondyls *Benthosuchus* and *Wetlugasaurus*, and described their connection with a fine, anastomosing network of capillaries in the superficial cortex. The same author, however, reported the absence of this network in the superficial cortex of the temnospondyl *Platyoposaurus*, and the possible seymouriamorph *Enosuchus*, which might be a relict gephyrostegid (Bulanov, 2003).

Thin sections reveal that capillaries (primary vascular canals, *sensu* Francillon-Vieillot *et al.*, 1990) that may or may not form a network can be found mostly in the more interior part of the superficial cortex, whereas the most superficial portion of the cortex is mostly avascular, or is only penetrated by isolated capillaries (Witzmann & Soler-Gijón, 2008; Witzmann, in press). Therefore, in most cases, they do not extend to the superficial surface of the bone. The high density of pores that may be visible on the superficial surface in some individuals is often the result of weathering or 'etching' of the original bone surface.

SCULPTURAL DEVELOPMENT DURING PERIPHERAL BONE GROWTH

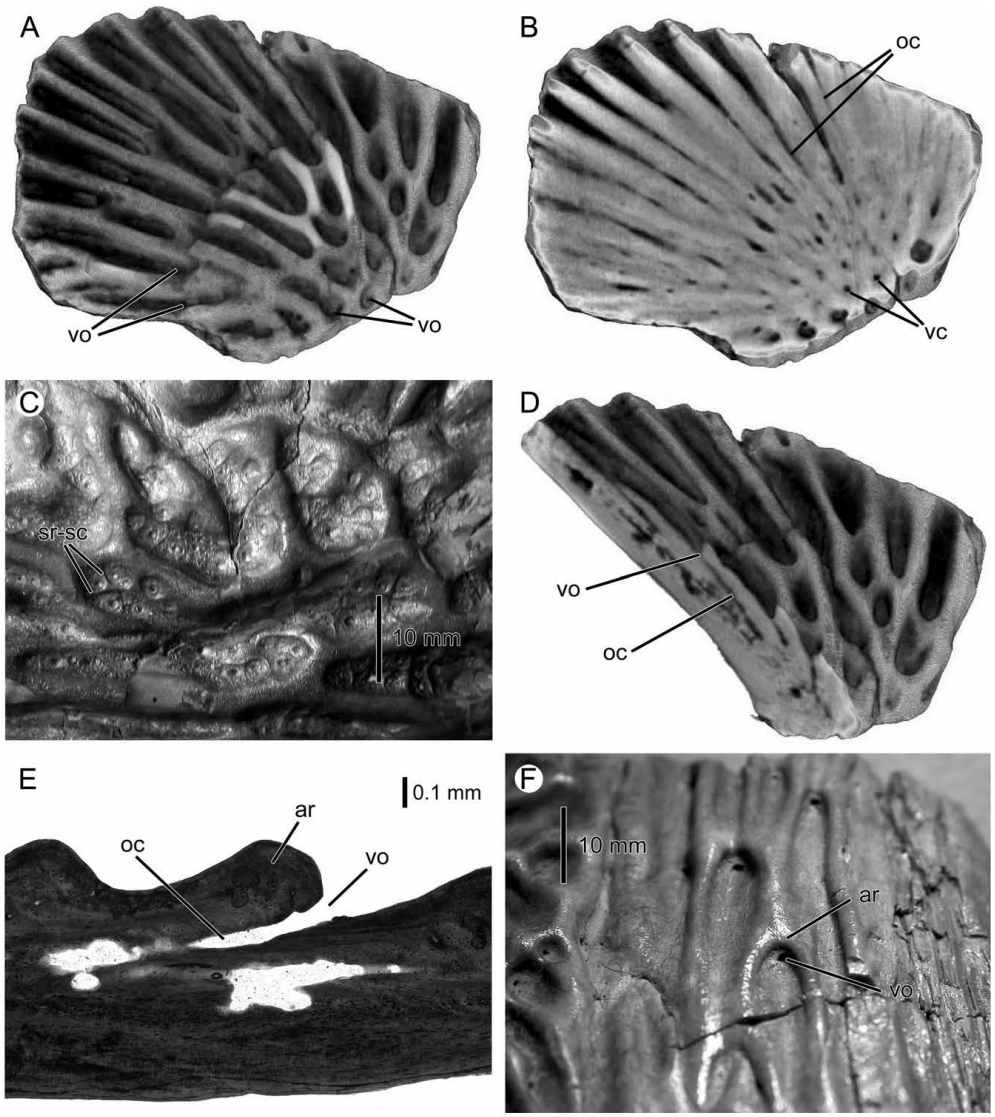
Intercalation of radiating sculptural ridges during growth

During peripheral bone growth, new radiating sculptural ridges were intercalated between the already existing ones so that the width of the furrows did not become larger in the bone periphery. The formation of additional ridges can proceed in different ways: a sculptural ridge may bifurcate symmetrically, and the opening of an oblique canal is situated in the branching point ('axilla'), immediately in front of the distal end of the old ridge (Fig. 6A). It is also possible that a sculptural ridge bifurcates asymmetrically: one lateral ridge may be more or less the continuation of the old ridge, or is only slightly bent laterad, whereas the ridge of the opposite side is distinctly diverted and bent (Fig. 6B, C). The vascular opening of an oblique canal is situated in the 'axilla' of this ridge immediately at the branching point, but not in front of the old ridge.

Bifurcation of ridges may also affect one and the same furrow from contralateral sides. Then, two ridges may fuse at roughly the midline of the furrow (Fig. 6D) and close the furrow. Sometimes, a sculptural ridge with an apparently abrupt origin is intercalated within a furrow between two ridges (Fig. 6E). Closer examination shows that such a ridge develops from an asymmetrical bifurcation of the old ridge, with the 'axilla ridge' of the corresponding vascular opening being suppressed and very low in height.

Development of cells from the radial furrows

The polygonal sculpture develops from the radial pattern by the formation of dividing walls within the



furrows, as first recognized by Bystrow (1935). Because sculptural development is most clearly visible in taxa with a regular polygonal sculpture, the formation of cells from radial ridges and furrows is described first for *M. fraasi*, before turning our attention to other forms in which sculpture is less regularly developed or tubercular.

An axilla ridge of a vascular opening that is located approximately in the middle of a sculptural furrow acts as a dividing wall within the furrow, and several dividing walls lead to the formation of sculptural cells. This takes place in the following way: prior to the formation of the dividing wall proper, the radial ridges broaden slightly at discrete points in the direc-

Figure 4. A, *Mastodonsaurus giganteus* (Stereospondyli, Capitosauroidea), MB.Am.1434. Neutron scan of clavicle. Dermal sculpture consists of polygonal ridges around pits in the ossification centre (lower right), and radially aligned sculptural ridges and furrows on the clavicular blade; vascular openings are visible in the pits, and in the furrows in front of the axilla ridges. B, same specimen, neutron scan. Horizontal section through the clavicle, showing that the large vascular canals open at a steep angle in the cells and open obliquely in the sculptural furrows. C, old specimen of *M. giganteus*, SMNS without number. Close-up of angular, showing smaller cells of a second order within larger cells. D, *M. giganteus*, MB.Am.1434. Neutron scan of the clavicle. Vertical section showing oblique canals opening to the bone surface in a sculptural furrow. E, *Captorhinus aguti* (Eureptilia, Captorhinidae), MCZ without number. Vertical thin section through a dermal skull bone. The large canal opens obliquely to the bone surface. F, *M. giganteus*, SMNS without number. Jugal in anterodorsal view with sculptural ridges and furrows, and axilla ridges proximal to the vascular openings. For abbreviations, see text.

tion of the furrow, or may be slightly bent in this direction (Fig. 6F). These are the points of intersection of the radial ridge with the future dividing wall. Each dividing wall grows slowly in height between these points proximal to the vascular opening. The formation of the dividing walls takes place often alternating between adjacent furrows (Fig. 6G). Through this process of compartmentalization, sculptural cells have developed from the radial ridges and furrows, and the slightly thickened parts of the ridges have become the nodal points. The newly developed cells have a rather quadrangular shape: they attain a polygonal (ideally hexagonal) outline during further appositional growth of the bone via a sidewards shift (oblique growth) of the nodal points (Fig. 6H). This oblique appositional growth can also be demonstrated by the successive growth marks in histological sections, with no evidence of surface resorption (Fig. 7A). The development described here applies in principle to all basal tetrapods that formed a polygonal sculpture. However, the sculpture is often not as regularly expressed as in *M. fraasi*, because of differences in the width and height of the ridges and nodal points, or because of variation in the width of the furrows or the size and regularity in outline of the cells.

In conclusion, the generalized sequence concerning the formation of cells from radial sculpture is as follows: (1) a radial sculpture of low ridges develops; (2) the ridges may broaden at discrete points or get slightly bent into the furrow; (3) dividing walls (as axilla ridges of vascular openings) are formed within the furrows between these discrete points, and lead to the formation of sculptural cells. This scheme also applies to taxa with tubercular sculpture; however, some aspects in their development are pronounced, whereas others are suppressed. Also, in the tubercular sculpture, low ridges are initially aligned radially, and show the same branching patterns as described above. During further growth, a thickening of discrete points on the sculptural ridges also occurs, but these points grow out subsequently to tubercles or protuberances. This development is visible, e.g. in *Chroniosaurus dongusensis* Tverdochlebova, 1972, from which a juvenile specimen (PIN 3585/124) possesses a sculpture that is composed primarily of radially aligned ridges (Fig. 7B). Tubercles are very few in number, in contrast to ontogenetically more advanced specimens (e.g. PIN 3713/11, 13) that have numerous distinct tubercles on these ridges (Fig. 7C). The tubercles of adjacent ridges may or may not be connected by rather low dividing walls in the sculptural furrows. The dividing walls often fail to develop, in contrast to the tubercle-bearing radial ridges, which gives this sculpture a larval or juvenile appearance.

Reduction of the number of ridges and furrows

The number of sculptural ridges and furrows can also be reduced in the bone periphery, but this is rather the exception. An example is the anterior part of the jugal in a specimen of *Mastodonsaurus*. A ridge bifurcates proximal to a vascular opening, and the 'axilla ridge' closes the neighbouring furrows of the old ridge, so that only a single, but broader furrow continues distally (Fig. 4F, middle). The sculptural ridges and furrows are roughly parallel with each other, as the jugal does not broaden anteriorly, and thus no new sculptural ridges have to be intercalated.

Lateral lines

Whereas the lateral line system is lost in amniotes, and therefore no vestiges are visible on the dermal bone sculpture of the parareptiles and basal eureptiles investigated, this mechanoreceptive organ left traces on the surface and within the dermal bones of many other basal tetrapods. In the finned stem tetrapods *Eusthenopteron* and *Panderichthys*, the lateral line system is located mostly in canals that course inside the bones, and open via sensory canal foramina to the bone surface (Jarvik, 1980; Vorobyeva & Schultze, 1991). The lateral lines of limbed stem tetrapods were partially enclosed in canals within bone (Beaumont, 1977; Smithson, 1980, 1982; Ahlberg, Lukševičs & Lebedev, 1994; Beaumont & Smithson, 1998; Clack, 2000), and extended in other parts in open sulci that are narrow, deeply incised

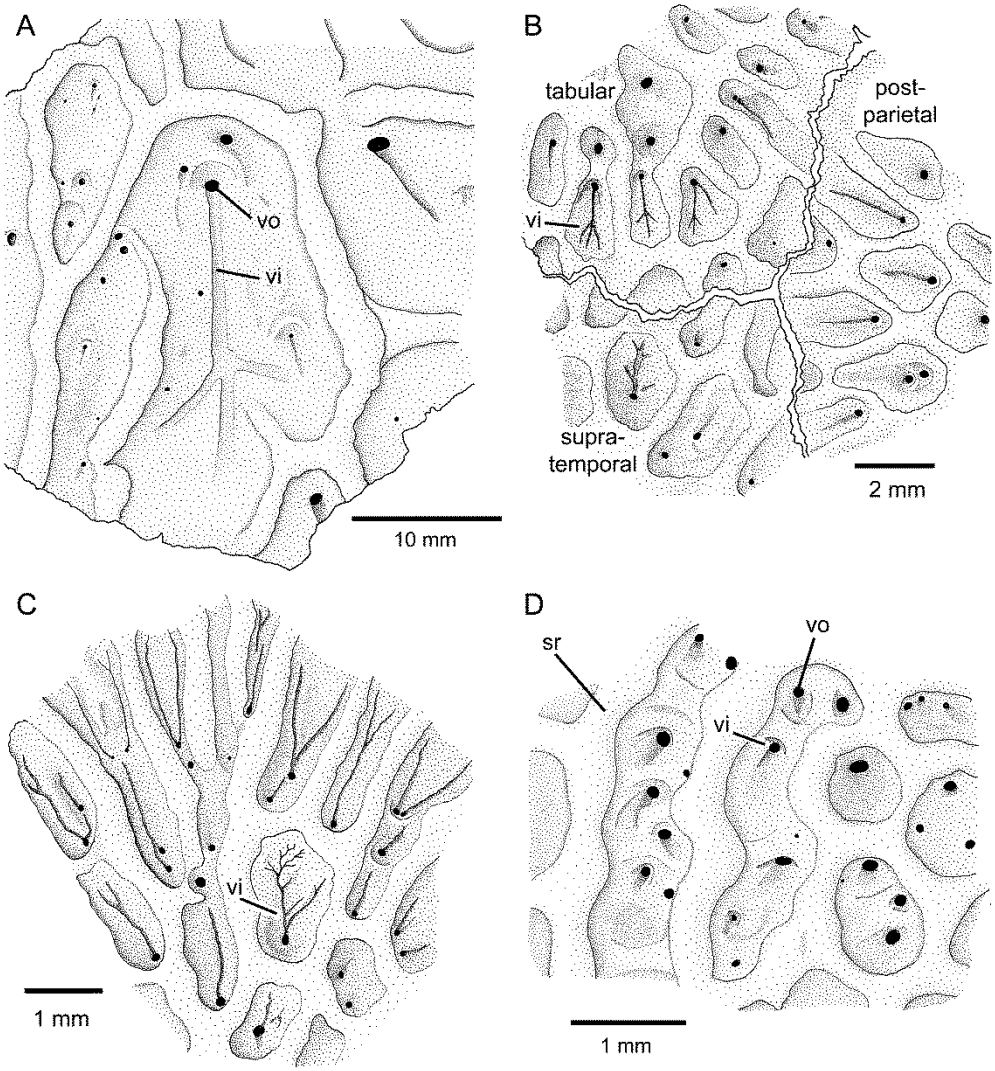


Figure 5. A–D, drawings of dermal sculpture and imprints of vessels. A, *Mastodonsaurus giganteus* (Stereospondyli, Capitosauroidea), SMNS 80878. Part of ?nasal with imprints of large, branching vessels. B, *Trimerorhachis insignis* (Temnospondyli, Dvinosauria), MCZ 8286. Dermal sculpture in the region of the junction between the tabular, supratemporal, and postparietal. C, *Cochleosaurus bohemicus* (Temnospondyli, Edopoidea), MB.Am.80. Dermal sculpture of postparietal lappet. D, *Captorhinus* sp. (Eureptilia, Captorhinidae), UCMP 202967. Part of dermal skull roof with cells and furrows. For abbreviations, see text.

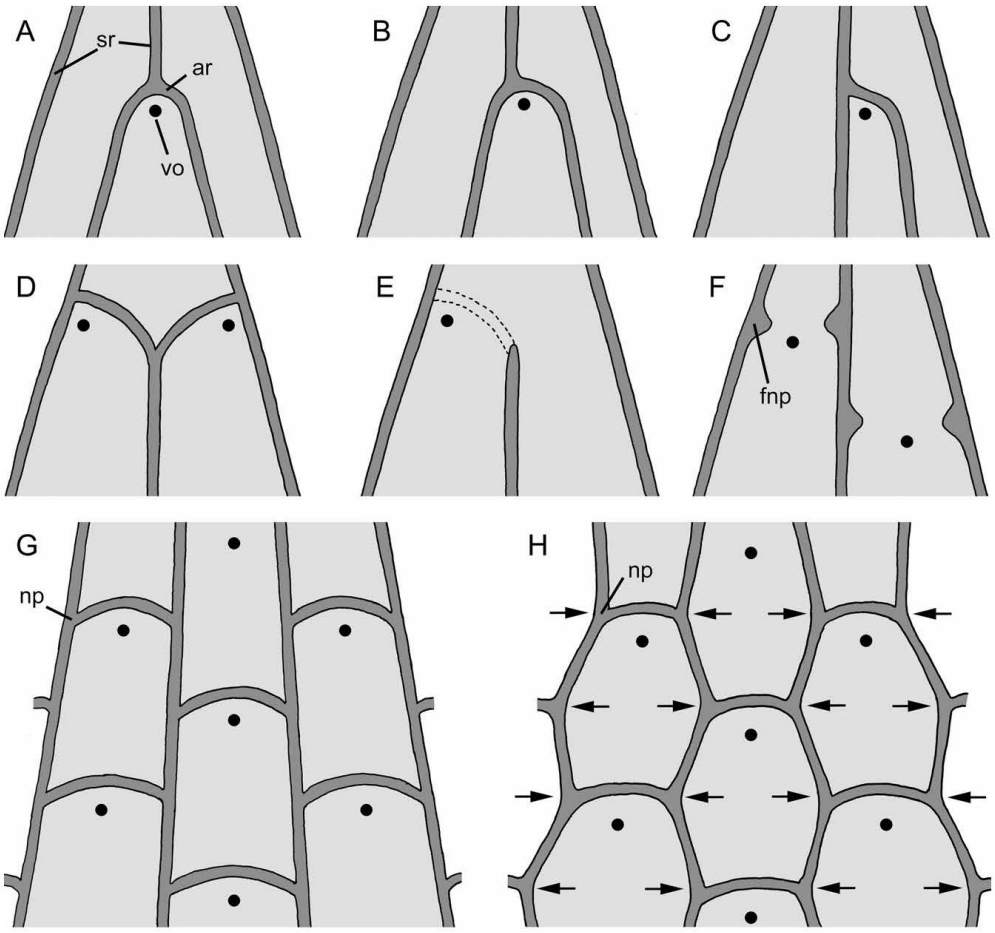


Figure 6. A–E, schematic drawings of formation of new sculptural ridges at the bone periphery during growth. A, the vascular opening is located directly in front of a sculptural ridge that bifurcates symmetrically. B–C, the vascular opening is located lateral to the sculptural ridge, and the bifurcation is asymmetric. D, bifurcation of ridges from contralateral sides fuse roughly at the midline of the furrow, and close the furrow. E, in an asymmetrical bifurcation of a sculptural ridge, the 'axilla ridge' of the corresponding vascular opening may be low or suppressed, giving the impression that the new intercalated ridge has an abrupt origin within the furrow. F–H, development of polygonal sculpture from the radial pattern. F, first, the radial ridges broaden slightly at discrete points in the vicinity of a vascular opening, or may be slightly bent in this direction. These are the points of intersection (nodal points) of the radial ridge with the future dividing wall. G, the dividing walls have grown slowly in height between these points proximal to the vascular openings; through this compartmentalization, sculptural cells have developed that have a rather quadrangular shape at first. H, during appositional growth of the bone, the cells attain a polygonal (ideally hexagonal) outline via a sidewards shift (oblique growth) of the nodal points (arrows). For abbreviations, see text.

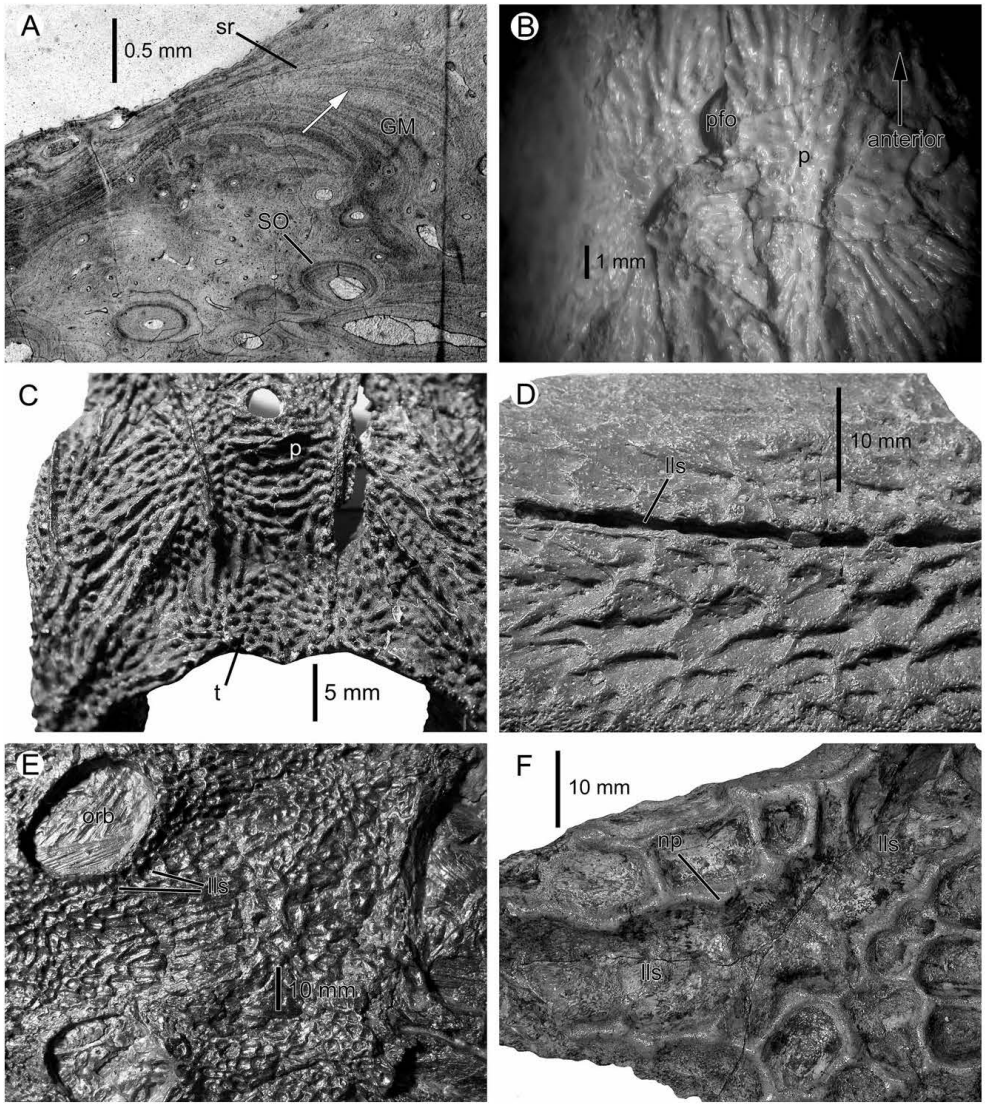


Figure 7. A, the oblique growth of nodal points and ridges as indicated in Figure 6H can be shown histologically. The growth marks indicate oblique appositional growth, and the arrow shows the direction of growth. B, *Chroniosaurus dongusensis* (Chroniosuchia, Chroniosuchidae), PIN 3585/124, juvenile specimen. The sculpture on the skull table consists primarily of radially aligned ridges, with very few tubercles. C, skull table of an ontogenetically advanced *Chroniosaurus dongusensis*, PIN 3713/11. The ridges bear numerous distinct tubercles. D, *Ventastega curonica* (stem tetrapod), PIN 54/180. Fragment of angular with deep, steep-walled lateral line sulcus that is partially enclosed within the bone. E, *Cheliderpeton latirostre* (Stereospondylomorpha, Intasuchidae), SMNS 91003. Posterior part of the skull with faintly impressed lateral line sulci posterior and medial to the orbits. F, *Metoposaurus fraasi* (Stereospondyli, Trematosauroidea), UCMP 27103. Prefrontal bearing a broad lateral line sulcus. For abbreviations, see text.

and have steep, smooth lateral walls (Fig. 7D). Although large vascular openings are present on the bottom of the sulci, they do not show any traces of compartmentalization by dividing walls.

In many aquatic more crownward tetrapods (temnospondyls, lepospondyls, and embolomeres), the lateral lines are developed within furrows that are integrated into the 'normal' sculpture, as they exhibit subdued sculptural ridges on their bottom, and the nodal points of these ridges are connected with the ridges of the adjacent sculptured area. Therefore, these lateral line sulci can be designated as suppressed sculpture, and the sulci may vary from more or less continuous lines to elongate pits. Their depth also varies, from slightly deeper than the sculptural pits and grooves, and thus hardly visible, e.g. in *Platyoposaurus* (Bystrow, 1935) or *Cheliderpeton* (Fig. 7E), to much more deeply incised, as in *Nigerpeton* (Steyer, Damiani & Sidor, 2006) or several taxa of stereospondyls *s.s.* (Fig. 7F). In many taxa like *Cochleosaurus*, zatracheids, and adult eryopids, traces of lateral lines are not visible (Boy, 1990; Schoch, 2002; Sequeira, 2004; Witzmann & Schoch, 2006), but the absence of sulci does not necessarily imply that the lateral line system was absent, as their impression on the bone surface might also depend on the thickness of the integument (Boy, 1972; Witzmann, 2006, 2007). Recently, Warren (2007) reported on an enclosed canal in the jugal and quadratojugal of the Early Carboniferous stem tetrapod *Ossinodus*. She interpreted this canal as part of the quadratojugal ramus of the sensory canal system. Based on this interpretation, Warren (2007) argued that enclosed lateral lines may have also been present in several temnospondyls that show no vestiges of sulci on the superficial bone surface, as similar enclosed canals have been reported in *Edops*, *Chenoprosopus*, and *Eryops*. However, this interpretation remains doubtful, as no sensory canal foramina on the superficial bone surface are associated with the canals.

Interestingly, the lateral line becomes more conspicuous during ontogeny in basal stereospondylomorphs (Boy, 1988; Witzmann, 2006) and micromelerpetontids (Boy, 1972), but gets reduced in taxa with more terrestrial adults like *Onchiodon* (Boy, 1990). In contrast, the lateral lines are already conspicuous in the small growth stages of stereospondyls (Bystrow, 1935; Warren & Marsicano, 1998; Steyer, 2003). Clack (2002) pointed out that the open lateral line sulci in tetrapods are a paedomorphic trait with respect to the enclosed canals of their fish-like ancestors. In bony fishes, the canal neuromasts form superficially in the epidermis, and sink in a furrow formed by dermis and epidermis (Webb & Shirey, 2003). Subsequently, the walls of this furrow ossify, so that the neuromasts sit in a bony, open groove, and finally, an ossified canal roof is formed. A similar development can also be presumed for basal tetrapods, and this is supported by the lateral line ontogeny in the stem tetrapod *Greererpeton*, in which the lateral line grooves of juveniles became increasingly roofed by bone in the adult phase (Godfrey, 1989). Therefore, in many tetrapods with very faintly impressed sulci, the neuromasts were probably situated far superficially in the skin, and this resembles a 'larval' or 'juvenile' condition. In many Late Permian and Mesozoic temnospondyls, the lateral line sulci have again become deeper and more conspicuous compared with most Permo-Carboniferous forms, either because the neuromasts sank deeper into the skin, or because they retained a more superficial position, and the skin became thinner (see Discussion).

DIFFERENTIATION OF SCULPTURAL PATTERNS BY PCA ANALYSIS

Results

The results of the PCA are illustrated (Fig. 8) using the first two principal component axes (PC1 and PC2). The first principal component axis (PC1) extracted from the data matrix has an eigenvalue of 78.8, and accounts for 38.5% of the variance. The second principal component axis (PC2) possesses an eigenvalue of 42.7, and explains 20.9% of the variance.

In general, a high negative value of PC1 ('on the left' in the diagram) represents a rather irregular and coarse sculpture, with differences in height and width of ridges, ridges that are broader than half the diameter of the cells, and a more tubercular sculpture, whereas a high positive value represents a more regular sculpture (rather constant height and width of the sculptural ridges) and ridges that are mostly narrower than half the diameter of the appertaining cells (Table 1). A positive (or slightly negative) value of PC1 plus a negative or slightly positive value of PC2 indicates that sculptural cells are hexagonal rather than rounded.

Taxa with a high positive value of PC2 ('on the top' in the diagram) have lateral lines enclosed in bone, with sensory canal foramina leading to the bone surface, and deeply incised sulci with steep walls; taxa with lower PC2 values have lateral line sulci that consist morphologically of suppressed sculpture, and in taxa with a high negative value of PC2, no sulci or sensory canal foramina can be detected on the superficial bone surface.

Panderichthys plus the limbed stem tetrapods are well separated from the other groups by a larger value of PC2 because of their lateral line morphology. *Greererpeton* and *Acanthostega* possess the most 'regular' sculpture of stem tetrapods, whereas *Pan-*

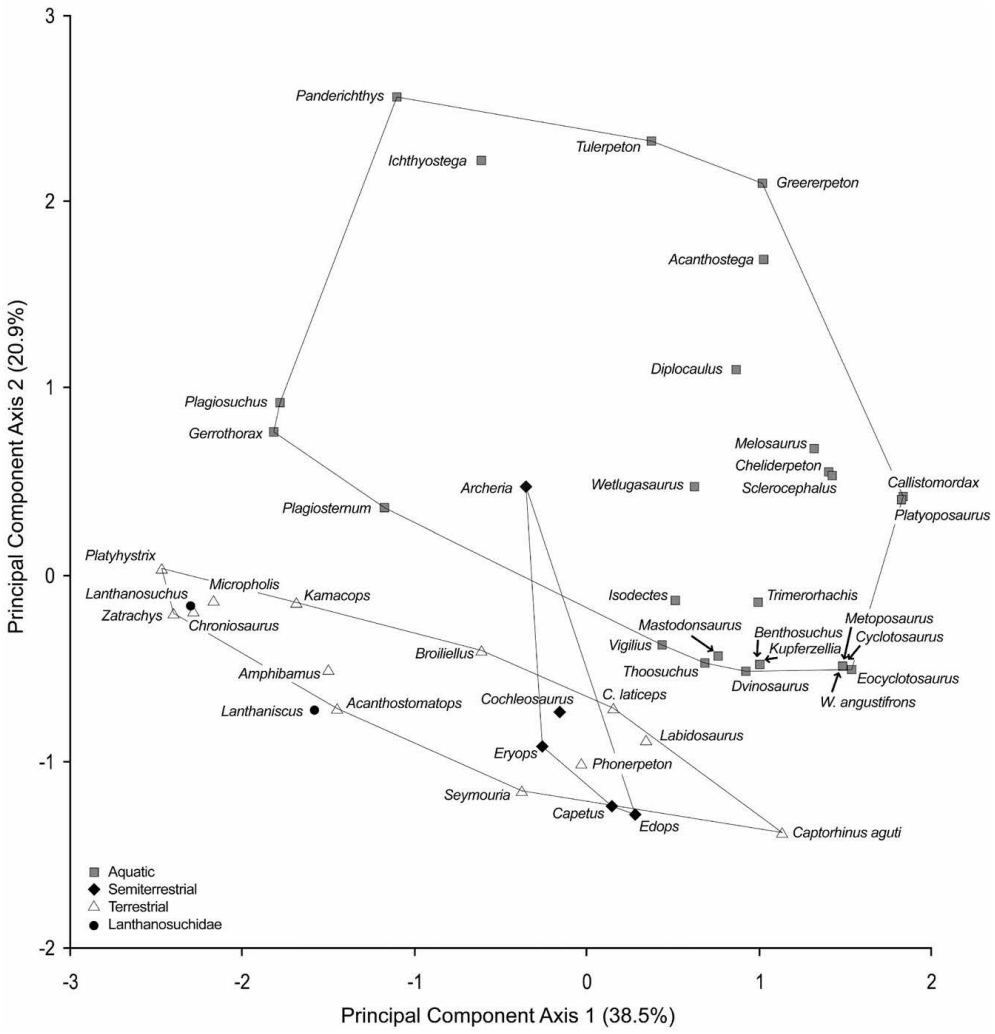


Figure 8. Principal component analysis of 47 taxa of basal tetrapods based on the 12 characters defined in Appendix 2 (nominal data). The convex hulls cover taxa with the same presumed life habit. The criteria for the presumed life habit of each taxon plus references are listed in Appendix 4.

derichthys and *Ichthyostega* are more irregular and tubercular (smaller values of PC1). All representatives of the stereospondylomorphs (excluding the Plagiosauridae, see below) have positive values of PC1, showing a rather 'regular' sculpture. The dvinosaurs (*Trimerorhachis*, *Dvinosaurus*, and *Isodectes*) plot out in the region of the Stereospondyli *s.s.*, because of their more regular sculpture. All representatives of the eryopids, zatracheids, and dissorophoids have negative values of PC1, and those taxa with the most irregular and rugose sculpture have the highest negative values (*Zatrachys*, *Platyhystrix*, and *Micropholis*). Edopoids and *Capetus* (probably a basal stereospondylomorph, see Schoch & Milner, 2000) occupy an

Table 1. Factor loading of the principal component analysis of 47 taxa of basal tetrapods, based on the 12 characters defined in Appendix 2 (nominal data)

Character	PC1	PC2
1	0.24	–0.05
2	0.22	–0.09
3	–0.49	0.01
4	0.30	–0.17
5	–0.30	0.14
6	–0.13	–0.05
7	0.05	–0.02
8	0.08	–0.02
9	–0.07	–0.03
10	–0.49	0.34
11	–0.36	–0.90
12	–0.29	0.11

intermediate position between eryopids, zatracheids, and dissorophoids on the one hand, and dvinosaurians and stereospondylomorphs without plagiosaurids (Capitosauroidea/Trematosauroidea, basal stereospondylomorphs) on the other. The plagiosaurids show high negative values, but all three taxa are well separated from the eryopids, zatracheids, and dissorophoids. *Plagiosuchus* and *Gerrothorax* with pronounced tubercles have higher negative values of PC1 than *Plagiosternum*, the sculpture of which is polygonal rather than tubercular.

The lepospondyl *Diplocaulus*, which has a sculpture of regular rounded cells, has positive PC1 values, and lies in the region of the stereospondylomorphs. The embolomere *Archeria* and the seymouriamorph *Seymouria* have intermediate values of PC1, whereas the chroniosuchian *Chroniosaurus* has one of the highest negative PC1 values in the sample. Laurin (2000) suggested that chroniosuchians might be relict embolomeres.

The captorhinids have a rather regular sculpture, which is indicated by the positive PC1 values that are comparable with dvinosaurians. The lanthanosuchids possess an irregular, very rugose, and tubercular sculpture, and are thus highly negative on PC1.

Is there a phylogenetic signal of dermal sculpture?

The morphospace occupation of stem tetrapods and temnospondyls in the PCA reflects the phylogenetic relationships of the different taxa to a certain degree. The stem tetrapods lie together (although they are certainly a paraphyletic assemblage), and *Eryops*, zatracheids, and dissorophoids are well separated from the Stereospondylomorpha. However, the highly derived plagiosaurids cannot be referred to one of these groups in the diagram. The Edopoidea lie between the eryopids, zatracheids, and dissorophoids on the one hand, and the Stereospondylomorpha (without plagiosaurids) on the other. The dvinosaurians lie close together, but overlap with the Stereospondyli *s.s.* When stem amniotes and basal amniotes are included, the picture is more complex. The far distantly related nectridean lepospondyl *Diplocaulus* lies close to the stereospondylomorphs, and the lanthanosuchid parareptiles lie next to the dissorophoids with a coarse sculpture. The captorhinids are located next to dvinosaurians and Stereospondyli *s.s.* This shows that the dermal sculptural pattern is of limited use to distinguish larger groups of basal tetrapods, but is suited to distinguish some of the main temnospondyl lineages.

A test for phylogenetic significance was carried out for each of the 12 characters of dermal sculpture that were defined for the PCA (see Material and methods). A significant phylogenetic signal is detectable for characters 1 ($P = 0.0022$), 2 (0.0016), 5 (0.0074), 6 (0.0068), 10 (0.0008), 11 (0.0000), and 12 (0.0062) (Figs 9, 10). The remaining characters turn out to be phylogenetically insignificant. This test shows that the regularity of sculpture (constancy in width and height of ridges, and in width of nodal points, outline of polygons, presence or absence of pronounced tubercles) as well as the lateral line morphology are phylogenetically significant. Character 6 refers to the presence or absence of dominating sculptural ridges that run over a long distance from nodal point to nodal point, and on more than one bone: such ridges can only be found in lanthanosuchids and zatracheids. The failure to test for phylogenetic significance in the remaining characters might be explained as follows. Character 3 describes the height of the sculptural ridges with respect to the nodal points. It is apparently easy to transform the polygonal into the tubercular pattern through evolution by enlargement and suppression, respectively, of the connecting sculptural ridges between the nodal points. This is shown, for example, by the independent development of tubercular sculpture within plagiosaurids, amphibamids (*Micropholis*), and chroniosuchians (*Chroniosaurus*). Character 4 shows that the width of the sculptural ridges with respect to the polygons is quite variable, and this also holds true for character 7, the morphology of the dorsal surface of the ridges (broadly rounded or edged). Character 8, the presence of sculpture on the surface of all dermal bones of the skull or its absence/depression in certain regions of the skull, is phylogenetically insignificant, as regions of subdued sculpture occur in several distantly related forms, like *Tulerpeton*, *Cochleosaurus*, different stereospondylomorphs, dissorophoids, *Zatrachys*, and *Archeria*. Finally, the lack of phylogenetic significance for character 9 (sculpture consists mostly of

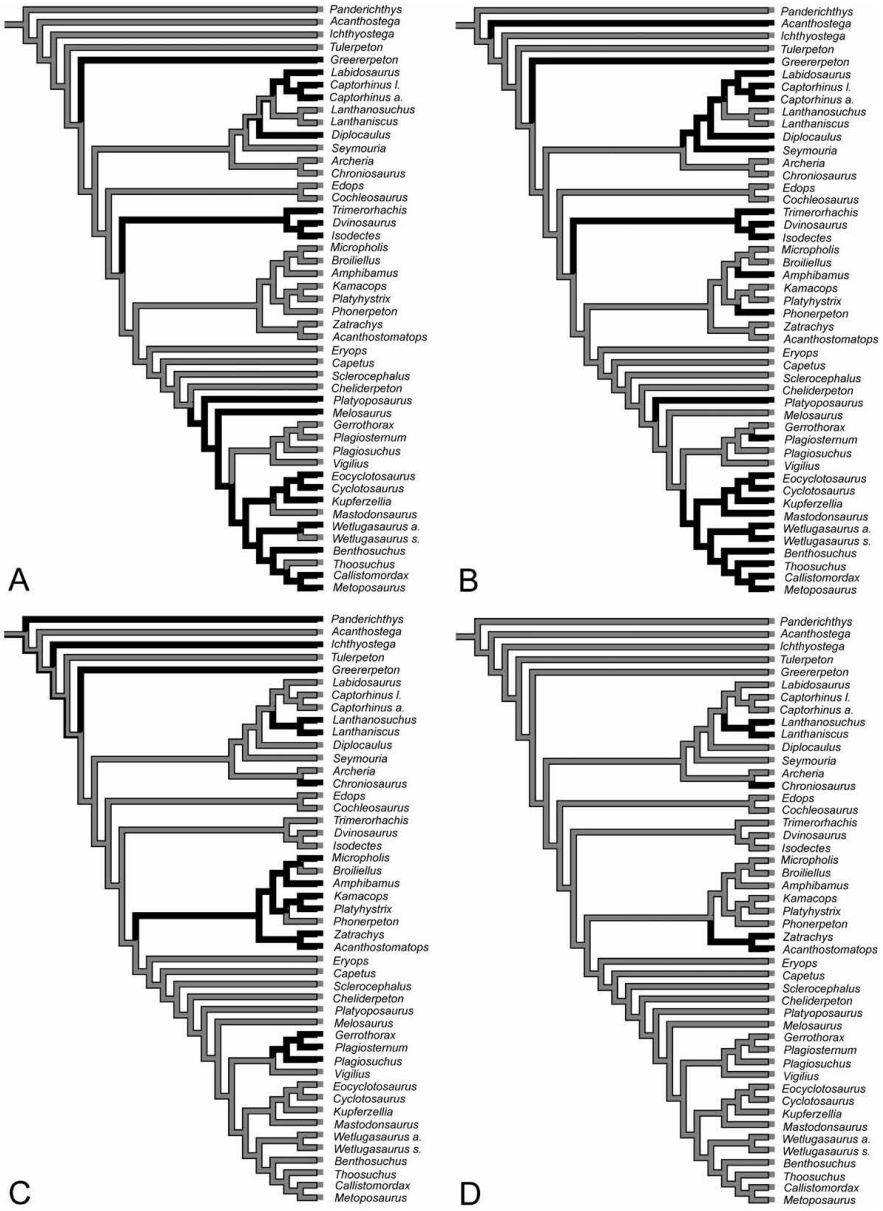


Figure 9. Dermal sculpture characters displaying a phylogenetic signal mapped on the reference topology. Reference topology based on Ruta *et al.* (2003), Ruta & Coates (2007), Schoch & Milner (2000), and Yates & Warren (2000). A, character 1. B, character 2. C, character 5. D, character 6. Grey shading refers to character state 1; black shading refers to character state 2. For definition of characters, see Appendix 2.

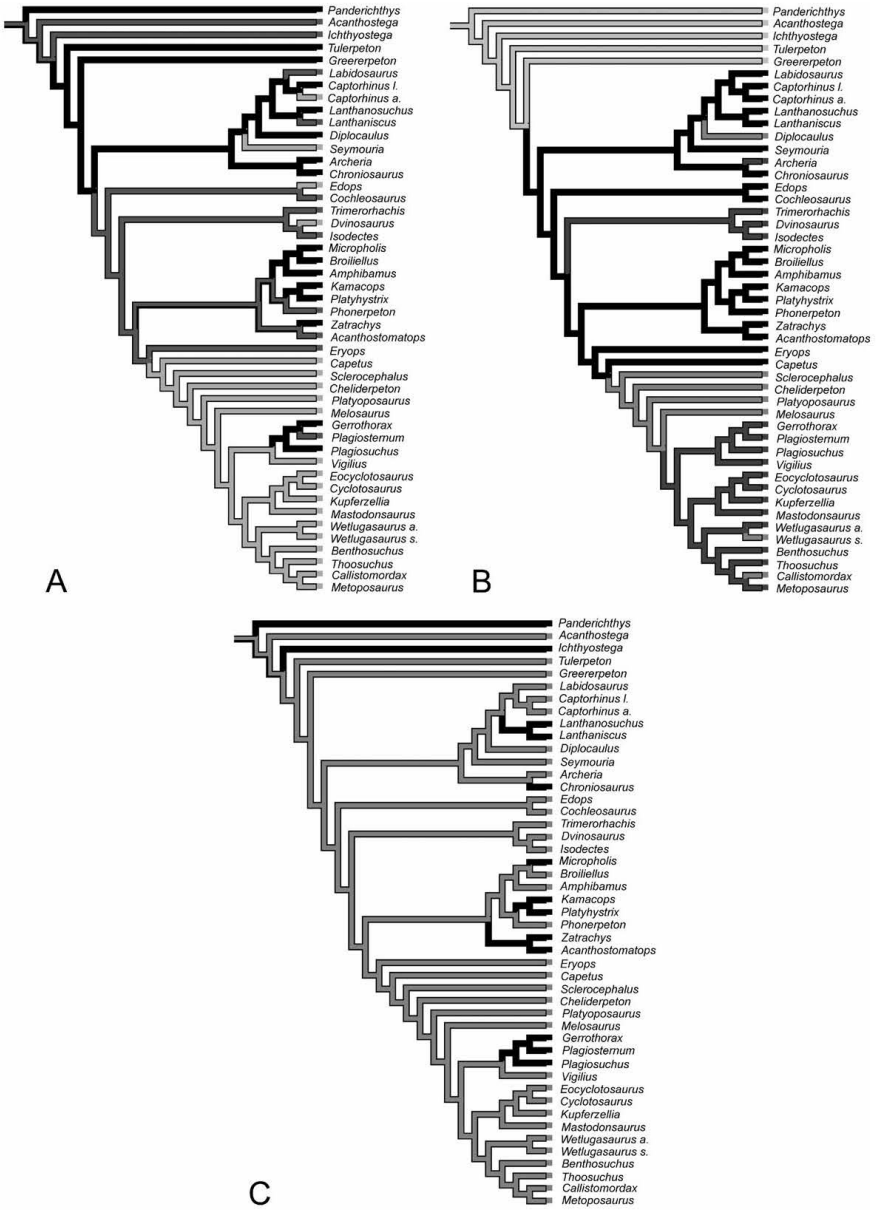


Figure 10. Reference topology with mapped dermal sculpture characters showing a phylogenetic signal, continued. A, character 10. B, character 11. C, character 12. For character 12, the coloration is similar to that in Figure 9, whereas for character 10 (four character states) and 11 (three character states), the lightest shading refers to character state 1, and the increasingly darker shadings refer to the ascending character states. For definition of characters, see Appendix 2.

polygons, or radial ridges and furrows) might be explained by ontogenetic variation, because polygonal sculpture develops ontogenetically out of the radial pattern, as shown above.

Mode of life and sculptural pattern

In the following analysis, we will assess whether there is a correlation between the lifestyle and the sculptural pattern of dermal bones. The criteria for the presumed lifestyle of each taxon plus references are listed in Appendix 4. The lifestyle of basal tetrapods, i.e. a more terrestrial or more aquatic mode of life, is often difficult to assess. The presence of lateral line sulci is a clear indicator that the animal lived a mainly aquatic lifestyle, whereas the absence of sulci does not necessarily mean that the lateral line organ was not developed (Laurin, Girondot & Loth, 2004; Vallin & Laurin, 2004). Further indicators of a water-dwelling existence are ossified branchial arches (ceratobranchials) and/or branchial dentition (Witzmann, 2004). In most terrestrial taxa, the limbs are long and robust, and the trunk and tail are short. In contrast, the trunk is often elongate, the limbs short, and the tail is developed as a long propulsive organ in primarily aquatic taxa. Furthermore, the overall degree of ossification of endochondral bones in the postcranial skeleton is much higher than in aquatic taxa (Schoch, 2002; Pawley & Warren, 2006; Pawley, 2007). This applies especially to the limb bones, and their muscular processes and condyles, the coracoid portion of the pectoral girdle, the pelvic bones, vertebrae, as well as carpals and tarsals. However, as outlined by Laurin *et al.* (2004), one has to consider the ontogenetic age of a basal tetrapod, as endochondral bones of larvae and juveniles, especially of temnospondyls, ossify slowly in ontogeny. Therefore, in the following, and in Appendix 4, only adult or presumably adult representatives of each taxon have been considered in the assessment of mode of life.

The result of the PCA analysis based on the sculptural morphology of the 47 taxa indicates the differences in their mode of life. Aquatic taxa are characterized by high PC2 values, terrestrial taxa are characterized by low PC2 values, and semi-terrestrial taxa fill the gap between aquatic and terrestrial taxa in morphospace. This pattern was also found as the result of a discriminant function analysis (DFA) of the three different groups. The sample size of each group, however, was too low to perform significance tests.

Concerning temnospondyls, it is striking that those taxa in the 'left lower corner' of the PCO diagram, i.e. with negative values of PC1 and low values of PC2 (Fig. 8), are forms that are interpreted as more terrestrial (zatracheids and dissorophoids) or semiterrestrial (*Eryops*). *Eryops* is regarded here as a semi-terrestrial temnospondyl. Although the postcranial anatomy suggests larger land excursions (Pawley & Warren, 2006), this animal still had to feed in water (Schoch, 2002, 2009). These more terrestrial and semiterrestrial forms possess a rather irregular, often coarse dermal sculpture, and lateral line sulci are not visible. The edopoid *Cochleosaurus*, which also lies in this region of morphospace, is problematic in this respect because its mode of life is still not entirely clear. The long, slender preorbital region suggests that it preyed mainly on aquatic vertebrates; however, the skull shows no traces of lateral line sulci or sensory canal foramina. *Cochleosaurus* has been found together with terrestrial reptiles and synapsids inside lycopsid stumps, suggesting that this temnospondyl undertook land excursions (Godfrey & Holmes, 1995; Schoch, 2009). Therefore, *Cochleosaurus* is regarded here as a semi-terrestrial form. Also, the basal stereospondylomorph *Capetus* can be interpreted as a semi-terrestrial animal that lacks lateral line sulci. Based on the superficial resemblance to *Alligator*, Sequeira & Milner (1993) regarded *Capetus* as a predator searching for prey both in water and on land. The remaining taxa of stereospondylomorphs investigated here can be interpreted as being predominantly aquatic (see Appendix 4). Schoch (2001) suggested that generally the stereospondylomorphs have a more regular sculpture, whereas most terrestrial temnospondyls bear a more irregular, often coarse dermal sculpture. Our results support his hypothesis to an extent, because an irregular pattern also appears in aquatic taxa, namely the plagiosaurids. This is also the case in some stem tetrapods (*Panderichthys*, *Ichthyostega*, and *?Tulerpeton*).

When the stem amniotes and basal amniotes are considered, the following picture arises: with its rather regular sculpture, *Diplocaulus* lies in the morphospace of stereospondylomorphs, and like most of them, it was a primarily aquatic animal. The semi-terrestrial embolomere *Archeria* has PC1 values similar to *Cochleosaurus* and *Eryops*, but with higher PC2 values (lateral line sulci). The chroniosuchian *Chroniosaurus* and the lanthanosuchid parareptiles lie close to the presumably terrestrial and semi-terrestrial temnospondyls (*Eryops*, zatracheids, and dissorophoids). Whereas chroniosuchians are interpreted as semi-terrestrial to terrestrial (Laurin *et al.*, 2004), the mode of life of lanthanosuchids is still not clear, as postcranial material is only very fragmentarily preserved. Watson (1954) interpreted *Lanthanosuchus* as an entirely aquatic animal that was not able to leave the water. Ivakhnenko (1980), in contrast, argued that the limb morphology of lanthanosuchids indicates a rather terrestrial mode of life. The sculptural pattern of lanthanosuchids could suggest a rather terrestrial mode of life. Among the terrestrial captorhinids,

Captorhinus laticeps (Williston, 1909) and *Labidosaurus* are located in the region of *Edops* and *Capetus*, whereas *Captorhinus aguti* (Cope, 1882) has a value of PC1 between those of the rather aquatic stereospondylomorphs *Benthosuchus* and *Melosaurus*. The location of *C. aguti* shows that regular sculpture is no general 'aquatic character' among basal tetrapods, although it is confined to primarily aquatic forms among temnospondyls.

DISCUSSION

THE SCULPTURAL PATTERNS AND THEIR PHYLOGENY

In basal tetrapods, the different sculptural patterns of the dermal bones can be traced back to a common basic pattern: the presence of nodal points and connecting ridges around dorsally concave areas (pits and furrows), in which large canals open to the bone surface. The diverse sculptural morphologies – regular, irregular, coarse, and tubercular – are all variations of the same theme, and depend on regularity and variation in height and width of the nodal points and ridges, and in size and shape of the enclosed pits and furrows. The angle of the large canals with respect to the bone surface determines if the sculptural pattern is more or less polygonal (high angle) or radial (low angle).

Although stem tetrapods like *Eusthenopteron*, *Panderichthys*, and *Ichthyostega* have tubercular nodal points, and mostly low or suppressed connecting ridges, it would be oversimplified to deduce that the tubercular sculptural pattern is the plesiomorphic state for tetrapods. The ridges may also be pronounced in the finned stem tetrapod *Eusthenodon* (Jarvik, 1952: figs 24, 28, 31a) so that parts of the sculpture appear irregularly polygonal. Furthermore, *Ventastega*, a stem tetrapod in which it is not clear that it possessed limbs (see Laurin, Girondot & de Ricqlès, 2000), and the limbed stem tetrapods *Acanthostega*, *?Tulerpeton*, and *Greererpeton*, have a clear polygonal sculpture. In spite of this, there seems to be a general trend in the evolution of tetrapods that the sculptural morphology gets more regular and more pronounced from the stem to the crown group, and the connecting ridges often get more conspicuous with respect to the nodal points. The basic sculptural pattern that can already be observed in finned and limbed stem tetrapods, with its association of sculptural elements and vascularization, is not only retained in basal non-amniote tetrapods, but also in parareptiles and basal eureptiles. As revealed by the test for a phylogenetic signal, the regularity of sculpture (i.e. the constancy in width and height of the sculptural elements, and the outline of cells), but also the morphology of the lateral lines (the degree of their depression on the bone surface, their continuous or discontinuous course), exhibit a significant phylogenetic signal.

Association of dermal sculpture with large blood vessels

As shown above, the pattern of the dermal sculpture reflects the course of the large vessels within the bone and within the dermis superficial to the bone surface. Within the bone, the large blood vessels course roughly radially in the direction of the bone periphery, to be confluent with the vessels of neighbouring bones and to supply the growing bone at the periphery. The vessels that led to the superficial bone surface, and left the bone via the vascular openings, coursed within the dermis near the bone surface, and were always accompanied by sculptural ridges and/or nodal points: either surrounded by a 'funnel' in polygonal sculpture, or flanked within a furrow by ridges in radial sculpture towards the bone periphery.

Ontogenetic data suggest that the vascular openings of the large canals on the bone surface developed prior to the formation of ridges and nodal points. Therefore, it is hypothesized that the development of vascular openings induced the formation of sculptural ridges, either proximally, as an 'axilla ridge', when the canals open obliquely to the surface, or around the opening, when the canals course approximately vertical to the bone surface. An increase in the number of vascular openings vertical to the bone surface within sculptural furrows accompanies the alteration of radial sculpture into the polygonal one.

Bone and dermis were obviously so closely integrated with one another (and the dermis overlying the ridges and tubercles was so thin, see below) that only the capillaries passed over the sculptural ridges and tubercles (as shown by imprints of vessels on the bone surface), and probably anastomosed with capillaries from the adjacent pit or groove along the ridges and tubercles. Because of this, the large vessels extending from bone into the dermis had to pass between the sculptural ridges and tubercles in furrows and pits, respectively.

POSSIBLE FUNCTIONAL AND BIOLOGICAL INTERPRETATIONS OF DERMAL SCULPTURE

In the following discussion, several hypotheses for the adaptive significance of dermal sculpture are surveyed, and we will discuss how our findings inform each of these.

Strengthening adaptation

Coldiron (1974) suggested that dermal bone sculpture functioned to withstand mechanical stress in basal tetrapods and crocodilians, especially during feeding (Coldiron, 1974). This interpretation is not convinc-

ing, as the direction of sculptural ridges in basal tetrapods does not reflect the direction of stress within the bone, but rather reflects the direction of blood vessels, and, as shown by Bystrow (1935), the direction of growth (see above). Furthermore, palpebral cups in certain microsaurs (Carroll, 1998), and osteoderms in temnospondyls as, for example, in *Gerrothorax* or *Peltobatrachus*, possess the same sculpture as the skull and pectoral girdle, but are not exposed to similar stress. Sculpture is only present in those parts of the bones that are directly overlain by the skin, and therefore, there must have been a direct correlation between soft-tissue integument and sculpture. As Seidel (1979) pointed out, the parts of the *Alligator* skull that sink deeper into the integument lose dermal sculpture, although the stress that acts on the bone remains the same. Furthermore, Schoch (2001) considered the height of the sculptural ridges and tubercles with respect to the overall thickness of the bone as being crucial for the effectivity of stress distribution. However, as he noted, the sculptural elements are rather low compared with the very thick dermal bones of many larger temnospondyls.

Co-ossification and cutaneous water loss

A rugose or pitted dermal sculpture reminiscent with that of basal tetrapods is present on the skull roofing bones of many extant anuran taxa. The formation of these sculptural ridges and spines may be associated with co-ossification of the bone surface with ossified parts of the skin in certain terrestrial anurans, and may reduce the extent of cutaneous water loss (Trueb, 1966, 1970, 1973; Seibert *et al.*, 1974). Seibert *et al.* (1974) suggested that the pronounced dermal sculpture in Palaeozoic and Mesozoic basal tetrapods might have been similarly connected with co-ossification between bone and dermis, and could have been an adaptation for a rather terrestrial existence. This interpretation, however, is not consistent with our data, as no indications of co-ossification between bone and the overlying dermis can be demonstrated histologically in the dermal bones of basal tetrapods in thin sections (Witzmann, in press), and dermal sculpture is present both in primarily aquatic and terrestrial basal tetrapods. Furthermore, the significance of co-ossified sculptured bones in anurans for water balance has been questioned in recent years. De Andrade & Abe (1997) were able to show that cranial co-ossification may have some water conservation effect in certain hylid taxa, whereas in other hylids an improved integumental isolation has the same or even better effect. Navas, Jared & Antoniazzi (2002) used simulated co-ossification in agar models, and found that water loss is only reduced by co-ossification to a minor degree.

Indicator of metamorphosis during ontogeny

Boy & Sues (2000) discerned different growth phases in certain temnospondyls on the basis of the outer morphology of dermal sculpture. These authors found the development of polygonal sculpture to be synchronous with a remodelling of the hyobranchial apparatus (resorption of branchial dentition, ossification of the basibranchial), and thus considered it to be a metamorphic feature. This holds true for taxa like eryopids (Boy, 1990; Witzmann, 2005), zatracheids (Witzmann & Schoch, 2006), micromelerpetontids (Boy, 1995; Witzmann & Pfretzschner, 2003), and the branchiosaurid *Apateon gracilis* (Credner, 1881; Werneburg, 1991; Schoch & Fröbisch, 2006). However, basal tetrapods like *Acanthostega* (Clack, 2000) and the colosteids (Smithson, 1982; Hook, 1983; Lebedev & Coates, 1995), which retain gill-breathing as adults, also develop polygonal sculpture on their dermal bones, and this is also the case in temnospondyls like *Uranocentrodon* (Van Hoepen, 1915; Schoch, 2002) and *Trimerorhachis* (Case, 1935), which maintain a 'larval' hyobranchium throughout life history. Similarly, basal stereospondylomorphs like *Sclerocephalus* (Schoch, 2003; Schoch & Witzmann, 2009a), *Cheliderpeton* (Schoch & Witzmann, 2009b), and *Archegosaurus* (Witzmann, 2006) develop a polygonal sculpture in spite of the retention of a branchial dentition during a long phase in ontogeny. This indicates that the sculptural pattern is a doubtful indicator of metamorphosis in most basal tetrapod taxa.

Integration of bone–dermis contact

In his 'Review of the Labyrinthodontia', Romer (1947) presumed that dermal bone sculpture caused a tighter attachment of skin to the underlying bone, and similarly, Bossy & Milner (1998) tentatively presumed an integration between bone and dermis in sculptured regions of the skull in nectrideans and other basal tetrapods. Indeed, histological thin sections of basal tetrapod dermal bones show strong, well-mineralized Sharpey's fibres, which are densely arranged especially in the sculptural ridges and tubercles, suggesting a tight anchorage of the dermis to the superficial bone surface in the living animal (Fig. 11A, B; Witzmann & Soler-Gijón, 2008). The Sharpey's fibres represent extraneous, pre-existing fibres of the dermis that became progressively incorporated in bone during its growth. It can be assumed that the Sharpey's fibres in basal tetrapods were interwoven with the fibres of the dermis, and were possibly extended to the epidermal–dermal boundary, analogous with the situation in the scales of many teleosts (Sire, 1985, 1986), and in the osteoderms of lizards (Zylberberg & Castanet, 1985; Levrat-Calviac & Zylberberg, 1986) and xenarthran mammals (Hill,

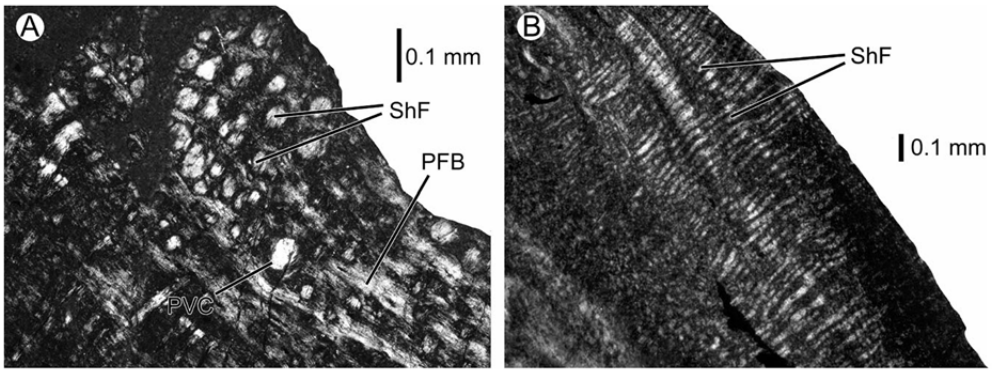


Figure 11. Thin sections of sculptural ridges showing mineralized Sharpey's fibres penetrating the bone. A, *Chenoprosopus milleri* (Temnospondyli, Edopoidea), UCMP 41104. The strong Sharpey's fibres are obliquely cut. B, *Plagiosternum granulosum* (Stereospondyli, Plagiosauridae), SMNS without number. The Sharpey's fibres are densely arranged. For abbreviations, see text.

2006). Furthermore, metaplastic tissue can be demonstrated in dermal bones of various basal tetrapod taxa (Witzmann & Soler-Gijón, 2008); Witzmann, in press). A mechanical advantage of metaplastic bone is a firm connection between bone and overlying soft tissue, as the collagen fibres of the attached soft tissue are confluent with the collagen fibres within the metaplastic bone (Haines & Mohuiddin, 1968).

The association of the sculptural ridges (whatever the pattern) with the large blood vessels that left the superficial bone surface by vascular openings might suggest that the sculptural ridges and nodal points acted as a protection for these vessels against mechanical damage like abrasion or pressure from the outside, as the large vessels always lie *between* the sculptural elements, and never on top of them. The coarser sculpture, with the more pronounced sculptural tubercles, in many rather terrestrial taxa might have provided enhanced resistance against mechanical damage of the vessels (and probably also of nerves and glands) on land, and the protuberances seen in zatracheids and lanthanosuchids might have served for defence against predators. A counter example, however, is the plagiosaurid *Plagiosuchus*, which is a primarily aquatic temnospondyl with a very pronounced sculpture consisting of strong ridges and high tubercles. Possibly the strengthening of the skin in this temnospondyl was required for certain ecological reasons, which is supported by the presence of a rather thick layer of mineralized nodules in the skin of the postcranium. This layer is reminiscent to some degree of the mineralized Eberth–Kastschenko layer in the dermis of several extant anuran taxa (Witzmann & Soler-Gijón, 2008).

Dermal sculpture and thickness of the overlying skin

Interestingly, the dorsally concave parts of the skull in basal tetrapods are lightly sculptured or sometimes even smooth, whereas the exposed regions (dorsally convex parts or the snout margins) are strongly sculptured, with well-developed ridges and, therefore, deep polygons. Clack (1998) presumed that in the Carboniferous stem tetrapod *Crassigyrinus*, the overlying skin was thicker in the dorsally concave parts than in the stronger sculptured, upraised areas. Carroll (1998) reported raised rims on the orbital margins in 'microsaurs' with unsculptured dermal skull bones, and similarly suggested a thick layer of connective tissue on the bones in the living animals. Another example is the dorsal osteoderms of *Plagiosuchus*, which have a rugose, albeit unsculptured superficial surface (Witzmann & Soler-Gijón, 2008). The rather thick layer of mineralized nodules superficial to the osteoderms (and also superficial to the ventral gastral scales) indicates that these osteoderms were located deep within the dermis (probably the stratum compactum), whereas the mineralized nodules were situated in the superficial part of the dermis (probably the stratum spongiosum) (Witzmann & Soler-Gijón, 2008). The mineralized nodules are absent, superficial to the sculptured dermal bones of *Plagiosuchus* (dermal skull roof, mandible, and dermal pectoral girdle), indicating that the sculptural ridges and tubercles extended into the superficial part of the dermis (i.e. the region that was probably occupied by the nodules in the postcranial skin). Further support for a rather thin integument over sculptured dermal bones in basal tetrapods is derived from the ontogeny of

lateral line sulci in aquatic Permo-Carboniferous temnospondyls. Small growth stages exhibit almost no traces of lateral line sulci on the dermal skull bones, whereas they become more distinct and more deeply impressed during further growth (Boy, 1972, 1988; Witzmann, 2006). This might be interpreted as follows. The skin may have been proportionally thicker relative to bone thickness (including the sculptural relief) in early growth stages, so that the lateral lines did not contact the surface of the bones. During further ontogeny, the bone sculpture was intensified at the expense of the relative thickness of the overlying dermis, and thus the lateral lines came to lie on the bone surface. However, alternatively, it cannot be ruled out that the neuromasts of the lateral line system sank deeper into the skin during ontogeny.

An extant analogon to basal tetrapods might be the sculptured cranial bones of certain extant anurans, for which Trueb (1966) was able to show that the dermis is distinctly thinner over sculptured than over smooth bone. However, even if the skin was thinner over stronger sculptured regions in basal tetrapods, the top of the ridges and tubercles did not extend up to the epidermis, but was still covered by superficial dermis, as thin sections and SEM show that strong bundles of Sharpey's fibres penetrate the surface of the sculptural elements (Witzmann & Soler-Gijón, 2008; Witzmann, in press). The subdued sculpture immediately next to the margins of the upper and lower jaw in a variety of basal tetrapods is interesting. Possibly these regions represent the origin of fleshy lips, which might have aided the directed inflow of water during suction while feeding in water, analogous with extant water-dwelling amphibians (Matthes, 1934).

Cutaneous respiration

Bystrow (1947) assumed that the vascularization of the dermal bones and overlying skin served for cutaneous respiration. He based his assumption not on the large vessels that opened within the sculptural cells and furrows, but explicitly on the above described capillary network or rete vasculosum. However, the superficial portion of the superficial cortex is often poorly vascularized by capillaries (simple primary vascular canals), or is even avascular, which renders a connection between cutaneous respiration and the capillaries doubtful. The fact that the more interior portion of the superficial cortex is mostly better vascularized by primary vascular canals and primary osteons than the poorly vascularized superficial portion, might indicate that the bone growth was faster in an earlier ontogenetic stage, and slowed down later (Witzmann, in press). Regarding the large number of vessels, and their ramification into small capillaries on the bone surface (as indicated by imprints), a respiratory function as found in lissamphibians cannot be ruled out. However, many basal tetrapods of the Palaeozoic and Mesozoic were distinctly larger than lissamphibians, and therefore had an unfavourable ratio of surface area to body volume. Furthermore, whereas the majority of lissamphibians have naked skin, the integument of Palaeozoic basal tetrapods possessed well-ossified, tightly set gastral and dorsal scales (Witzmann, 2007). Additionally, the presence of metaplastic tissue and numerous mineralized, strong Sharpey's fibres in the dermal bones indicate that the skin in these forms was rather dense. This renders a large-scale gas exchange function, as seen in lissamphibians, rather unlikely in most basal tetrapods, possibly with the exception of the often miniaturized, newt-like lepospondyls (Schoch & Carroll, 2003). As already suspected by Romer (1972), it has become more and more apparent in recent years that the small-growing lissamphibians with their mostly naked, moist skin are probably not an appropriate extant paradigm for basal tetrapods in this respect. Apart from the indications that the skin was quite dense and possessed often well-ossified dermal scales, there is evidence that the epidermis in basal tetrapods was rather similar to amniotes, in being more strongly cornified and more complex, compared with lissamphibians (Maddin, Musat-Marcu & Reisz, 2007). Also, the fact that many parareptiles and basal eureptiles exhibit the same patterns of dermal sculpture and vascularization argues against a primary respiratory function, as these amniotes almost certainly possessed a well keratinized integument.

Thermoregulation

A further possibility is that basal tetrapods might have used the well-vascularized skin for thermal regulation, in modifying heating and cooling rates by alteration of the blood flow through the skin, similar to extant crocodiles, in which sculptured dermal bones with numerous large canals opening to the surface are present (Seidel, 1979; Grigg & Seebacher, 2001). Thermoregulation via alteration of blood flow in the dermis is also common in other extant reptiles, e.g. squamates (Drane & Webb, 1980). When the animal is basking, an increase in cutaneous blood flow (by peripheral vasodilatation and higher heart rates) conducts the absorbed heat from the periphery to the core of the body. During cooling, the blood flow decreases (by peripheral vasoconstriction and lower heart rates), and the skin serves as a thermal insulator. This mechanism permits rapid heating when the animal is exposed to the sun, but slows down cooling when it has left its basking site (Grigg & Seebacher, 2001).

Carroll, Irwin & Green (2005) raised the idea that warming up in the radiant heat of the sun was the main selective factor for the acquisition of terrestriality in Devonian tetrapods, as it enabled them to search for prey at a higher metabolic rate when they returned to water, but these authors did not mention the possible role of dermal bone sculpture, and its association with large vessels for thermal physiology. Although thermoregulation was certainly performed to some degree on exposed parts of the body, it is difficult to imagine that thermoregulation was the adaptive significance of dermal bone sculpture in basal tetrapods, as in a variety of taxa there are areas of the skull in which dermal sculpture is subdued or even absent (see the examples mentioned above), and the blood supply of the dermis largely corresponds with that in sculptured areas. Furthermore, the dermal sculpture and the degree of vascularization of the skin is equally developed on the ventral side of the body (interclavicle, clavicular blades, and ventral side of mandibles) as on the dorsal side, and these areas were not exposed to the sun, and are thus hardly relevant for thermoregulation during basking.

CONCLUSIONS

The course of the large canals that carried blood within the dermal bones and opened to the superficial bone surface has determined the morphology and arrangement of the dermal sculpture in basal tetrapods. Large vessels that opened roughly vertically to the surface resulted in the formation of a more or less polygonal sculpture, whereas canals that opened obliquely in the direction of the bone periphery caused radially aligned ridges and furrows. Therefore, the morphology of dermal sculpture and vascularization are not separable. The regularity of the sculpture is phylogenetically significant, and reflects the mode of life of basal tetrapods to a certain degree.

As indicated by histological thin sections, the integument in sculptured basal tetrapods was consolidated by strong, mineralized Sharpey's fibres that penetrated the sculptural elements, and by the presence of metaplastic tissue in several taxa. The large vessels were not able to spread over the sculptural ridges and tubercles because of the tight integration of bone and dermis. Rather, they had to pass interosseously between them, in contrast to the capillaries. Therefore, as the alignment of the large vessels corresponds to the (radial) direction of growth of the particular skull bones, the morphology of the dermal sculpture necessarily reflects this pattern.

The vascularization of the bone surface and dermis might have been used for thermoregulation in some of the more terrestrial taxa, and, in small-growing forms, for cutaneous respiration to some extent, but this was certainly not a greater specialization of animals with sculptured dermal bones, as the dermis is not less vascularized in the forms in which sculpture is subdued or even absent. Rather, the large blood vessels represent the 'normal' supply of the dermis and the periosteum.

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REFERENCES

Ahlberg PE, Lukševičs E, Lebedev O. 1994. The first tetrapod finds from the Devonian (Upper Famennian) of Latvia. *Philosophical Transactions of the Royal Society london, Series B* **343:** 303–328.

Amalitzky WP. 1921. *Dvinosauridae: North Dvina Excavations of Prof. Amalitzky*. Petrograd: Russian Akademii Nauk.

Anderson JS, Reisz RR, Scott D, Fröbisch NB, Sumida SS. 2008. A stem batrachian from the Early Permian of Texas and the origin of frogs and salamanders. *Nature* **453:** 515–518.

Barkas TP. 1873. *Illustrated guide to the fish, amphibian, reptilian and supposed mammalian remains of the Northumberland Carboniferous strata*. London: Hutchings.

Beaumont EI. 1977. Cranial morphology of the Loxommatidae (Amphibia: Labyrinthodontia). *Philosophical Transactions of the Royal Society of London, Series B* **280:** 29–101.

Beaumont EI, Smithson TR. 1998. The cranial morphology and relationships of the aberrant Carboniferous amphibian *Spathicephalus mirus* Watson. *Zoological Journal of the Linnean Society* **122:** 187–209.

Berman DS, Reisz RR, Fracasso MA. 1981. Skull of the Lower Permian dissorophid amphibian *Platyhystrix rugosus*. *Annals of Carnegie Museum* **50:** 391–416.

Bossy KA, Milner AC. 1998. Order Nectridea Miall 1875. In: Wellnhofer P, ed. *Handbuch der paläoherpetologie*, Vol. 1. München: Verlag Dr. Friedrich Pfeil, 73–131.

Boy JA. 1972. Die Branchiosaurier (Amphibia) des saarpfälzischen Rotliegenden (Unter-Perm, SW-Deutschland). *Abhandlungen des Hessischen Landesamtes für Bodenforschung* **65:** 1–137.

Boy JA. 1978. Die Tetrapodenfauna (Amphibia, Reptilia) des saarpfälzischen Rotliegenden (Unter-Perm; SW-Deutschland). 1. *Branchiosaurus*. *Mainzer Geowissenschaftliche Mitteilungen* **7:** 27–76.

Boy JA. 1988. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstes Karbon-Perm). 1. *Sclerocephalus*. *Paläontologische Zeitschrift* **62:** 107–132.

Boy JA. 1990. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstes Karbon – Perm). 3. *Onchiodon*. *Paläontologische Zeitschrift* **64:** 287–312.

Boy JA. 1993. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstes Karbon – Perm). 4. *Cheliderpeton latirostre*. *Paläontologische Zeitschrift* **67:** 123–143.

Boy JA. 1995. Über die Micromelerpetontidae (Amphibia: Temnospondyli). 1. Morphologie und Paläoökologie des *Micromelerpeton credneri* (Unter-Perm; SW-Deutschland). *Paläontologische Zeitschrift* **69:** 429–457.

Boy JA, Sues HD. 2000. Branchiosaurs: Larvae, Metamorphosis and Heterochrony in Temnospondyls and Seymouriamorphs. In: Heatwole H, Carroll RL, eds. *Amphibian Biology 4. Palaeontology*. Chipping Norton: Surrey Beatty, 1150–1197.

Broili F. 1904. Stammreptilien. *Anatomischer Anzeiger* **25:** 577–587.

Bulanov VV. 2003. Evolution and systematics of seymouriamorph parareptiles. *Paleontological Journal* **37:** 1–105.

Bystrow AP. 1935. Morphologische Untersuchungen der Deckknochen des Schädels der Stegocephalen. 1. Mitteilung. Schädel der Stegocephalen. *Acta Zoologica (Stockholm)* **16:** 65–141.

Bystrow AP. 1938. *Dvinosaurus* als neotenische Form der Stegocephalen. *Acta Zoologica (Stockholm)* **19:** 209–295.

Bystrow AP. 1947. Hydrophilous and xerophilous labyrinthodonts. *Acta Zoologica (Stockholm)* **28:** 137–164.

Carroll RL. 1964. Early evolution of the dissorophoid amphibians. *Bulletin of the Museum of Comparative Zoology* **131:** 161–250.

Carroll RL. 1998. Order Microsauria Dawson 1863. In: Wellnhofer P, ed. *Handbuch der Paläoherpetologie*, Vol. 1. München: Verlag Dr. Friedrich Pfeil, 1–72.

Carroll RL, Irwin J, Green DM. 2005. Thermal physiology and the origin of terrestriality in vertebrates. *Zoological Journal of the Linnean Society* **143:** 345–358.

Case EC. 1910. New or little known reptiles and amphibians from the Permian (?) of Texas. *Bulletin of the American Museum of Natural History* **28:** 163–181.

Case EC. 1935. Description of a collection of associated skeletons of *Trimerorhachis*. *Contributions from the Museum of Paleontology, University of Michigan* **4:** 227–274.

Chinsamy A, Raath MA. 1992. Preparation of fossil bone for histological examination. *Palaeontographica Africana* **29:** 39–44.

Clack JA. 1998. The Scottish Carboniferous tetrapod *Crassigyrinus scoticus* (Lydekker) – cranial anatomy and relationships. *Transactions of the Royal Society of Edinburgh* **88:** 127–142.

Clack JA. 2000. The origin of tetrapods. In: Heatwole H, Carroll RL, eds. *Amphibian Biology 4. Palaeontology*. Chipping Norton: Surrey Beatty, 979–1029.

Clack JA. 2002. *Gaining ground. The origin and evolution of tetrapods*. Bloomington and Indianapolis: Indiana University Press.

Cloutier R, Ahlberg PE. 1996. Morphology, characters, and the interrelationships of basal sarcopterygians. In: Stiassny MLJ, Parenti LR, Johnson GD, eds. *Interrelationships of fishes*. San Diego, CA: Academic Press, 445–480.

Coldiron RW. 1974. Possible functions of ornament in labyrinthodont amphibians. *Occasional Papers of the Museum of Natural History of Lawrence* **33:** 1–19.

Cope ED. 1868. Synopsis of the extinct Batrachia of North America. *Proceedings of the Academy of Natural Sciences* **20:** 208–221.

Cope ED. 1877. Descriptions of extinct vertebrata from the Permian and Triassic formations of the United States. *Proceedings of the American Philosophical Society* **17:** 182–195.

Cope ED. 1878. Descriptions of extinct Batrachia and Reptilia from the Permian Formations of Texas. *Proceedings of the American Philosophical Society* **17:** 505–530.

Cope ED. 1882. Third contribution to the history of the Vertebrata of the Permian formation of Texas. *Proceedings of the American Philosophical Society* **20:** 405–461.

Cope ED. 1884. The Batrachosauria of the Permian Period of North America. *American Naturalist* **18:** 26–39.

Cope ED. 1895a. A batrachian armadillio. *American Naturalist* **29:** 998.

Cope ED. 1895b. The reptilian order Cotylosauria. *Proceedings of the American Philosophical Society* **34:** 436–457.

Cosgriff JW, Zawiskie JM. 1979. A new species of the Rhytidosteidae from the *Lystrosaurus* zone and a review of the Rhytidosteoidea. *Palaeontologica Africana* **22:** 1–27.

Credner H. 1881. Die Stegocephalen (Labyrinthodonten) aus dem Rothliegenden des Plauenschen Grundes. Zweiter Theil. *Zeitschrift der Deutschen geologischen Gesellschaft* **33:** 298–330.

Credner H. 1883. Die Stegocephalen aus dem Rothliegenden des Plauen'schen Grundes bei Dresden. Vierter Theil. *Zeitschrift der Deutschen geologischen Gesellschaft* **35:** 275–300.

Credner H. 1886. Die Stegocephalen aus dem Rotliegenden des Plauen'schen Grundes bei Dresden. Sechster Theil. *Zeitschrift der Deutschen Geologischen Gesellschaft* **38:** 567–633.

Damiani R, Schoch RR, Hellrung H, Werneburg R, Gastou S. 2009. The plagiosaurid temnospondyl *Plagiosuchus pustuliferus* (Amphibia: Temnospondyli) from the

Middle Triassic of Germany: anatomy and functional morphology of the skull. *Zoological Journal of the Linnean Society* **155:** 348–373.

De Andrade DV, Abe AS. 1997. Evaporite water-loss and oxygen uptake in two casque-headed tree frogs, *Aparasphenodon brunoi* and *Corythomantis greeningi* (Anura, Hylidae). *Comparative Biochemistry and Physiology Series A* **118:** 685–689.

DeMar R. 1968. The Permian labyrinthodont amphibian *Dissorophus multicinctus*, and adaptations and phylogeny of the family Dissorophidae. *Journal of Paleontology* **42:** 1210–1242.

Dias EV, Richter M. 2002. On the squamation of *Australerpeton cosgriffi* Barberena, a temnospondyl amphibian from the Upper Permian. *of Brazil. Anais da Academia Brasileira de Ciências* **74:** 477–490.

Dilkes D. 1990. A new trematopsid amphibian (Temnospondyli: Dissorophoidea) from the Lower Permian. *of Texas. Journal of Vertebrate Paleontology* **10:** 222–243.

Drane CR, Webb GJW. 1980. Functional morphology of the dermal vascular system of the Australian lizard *Tiliqua scincoides*. *Herpetologica* **36:** 60–66.

Efremov IA. 1929. *Benthosaurus sushkini*, ein neuer Labyrinthodont der permotriassischen Ablagerungen des Scharschenga Flusses, Nord-Düna Gouvernment. *Bulletin de l'Academie des Sciences de l'Union des Republiques Sovietiques Socialistes, Math and Natural Sciences* **1929:** 757–770.

Efremov IA. 1946. On the subclass Batrachosauria – a group of forms intermediate between amphibians and reptiles. *Bulletin of the Academy of Science of the USSR Section of Biological Sciences* **6:** 615–638. (in Russian).

Fraas E. 1889. Die Labyrinthodonten der schwäbischen Trias. *Palaeontographica* **36:** 1–158.

Fraas E. 1896. *Die schwäbischen Trias-Saurier nach dem Material der Kgl. Naturalien-Sammlung in Stuttgart zusammengestellt*. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.

Fraas E. 1913. Neue Labyrinthodonten aus der schwäbischen Trias. *Palaeontographica* **60:** 275–294.

Francillon-Vieillot H, de Buffrénil V, Castanet J, Geraudie J, Meunier FJ, Sire JY, Zylberberg L, de Ricqlès A. 1990. Microstructure and mineralization of vertebrate skeletal tissues. In: Carter JG, ed. *Biomineralization: Patterns and Evolutionary Trends*. New York: Van Nostrand Reinhold, 471–530.

Fritsch A. 1889. *Fauna der Gaskohle und der Kalksteine der Permformation Böhmens*, Vol. 2. Prag: Selbstverlag.

Frič A. 1876. Über die Fauna der Gaskohle des Pilsner und Rakonitzer Beckens. *Sitzungsberichte der Königlichen Böhmischen Gesellschaft der Wissenschaften* **1875:** 70–79.

Gastou S. 2007. A revision of the plagiosaurid *Plagiosternum granulosum* Fraas (Amphibia: Temnospondyli) from the Middle Triassic of Germany. Unpublished DES Report, Université Paris 6.

Godfrey S. 1989. Ontogenetic changes in the skull of the Carboniferous tetrapod *Greererpeton burkemorani* Romer 1969. *Philosophical Transactions of the Royal Society of London, Series B* **323:** 135–153.

Godfrey S, Holmes R. 1995. The Pennsylvanian temnospondyl Cochleosaurus florensis Rieppel, from the lycopsid stump fauna at Florence, Nova Scotia. *Breviora* **500:** 1–25.

Goldfuss GA. 1847. *Beiträge zur vorweltlichen Fauna des Steinkohlengebirges*. Bonn: Naturhistorischer Verein für die preussischen Rheinlande.

Grigg G, Seebacher F. 2001. Crocodilian thermal relations. In: Grigg GC, Seebacher F, Franklin CE, eds. *Crocodilian biology and evolution*. Chipping Norton: Surrey Beatty, 297–309.

Gross W. 1930. Die Fische des Mittleren Old Red Süd-Livlands. *Geologische und Paläontologische Abhandlungen. Neue Folge* **18:** 121–156.

Gubin YM. 1980. New Permian dissorophids of the Ural Forelands. *Paleontological Journal* **1980:** 88–96.

Haines RW, Mohuiddin A. 1968. Metaplastic bone. *Journal of Anatomy* **103:** 527–538.

Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* **4:** 9. Available at http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Hellrung H. 2003. *Gerrothorax pustuloglomeratus*, ein Temnospondyle (Amphibia) mit knöcherner Branchialkammer aus dem Unteren Keuper von Kupferzell (Süddeutschland). *Stuttgarter Beiträge zur Naturkunde Ser. B* **330:** 1–130.

Hennig W. 1966. *Phylogenetic Systematics*. Champaign, IL: University of Illinois Press.

Hill RV. 2006. Comparative anatomy and histology of xenarthran osteoderms. *Journal of Morphology* **267:** 1441–1460.

Holmes R. 1989. The skull and axial skeleton of the Lower Permian anthracosauroid amphibian *Archeria crassidisca* Cope. *Palaeontographica* **207:** 161–206.

Hook RW. 1983. *Colosteus scutellatus* (Newberry), a primitive temnospondyl amphibian from the Middle Pennsylvanian of Linton, *Ohio. American Museum of Natural History Novitates* **2770:** 1–41.

von Huene F. 1922. Beiträge zur Kenntnis der Organisation einiger Stegocephalen der schwäbischen Trias. *Acta Zoologica (Stockholm)* **3:** 395–460.

Huxley TH. 1859. On some amphibian and reptilian remains from South Africa and Australia. *Quarterly Journal Geological Society London* **1859:** 52–56.

Ivakhnenko MF. 1980. Lanthanosuchids from the Permian of the East European Platform. *Paleontological Journal* **14:** 80–90.

Jaeger GF. 1828. *Über die fossile Reptilien, welche in Württemberg aufgefunden worden sind*. Stuttgart: Metzler.

Jarvik E. 1952. On the fish-like tail in the ichthyostegid stegocephalians with descriptions of a new stegocephalian and a new crossopterygian from the Upper Devonian of East Greenland. *Meddelelser Om Grønland* **114:** 1–90.

Jarvik E. 1980. *Basic structure and evolution of vertebrates*, Vol. 1. London: Academic Press.

Jordan H. 1849. Ergänzende Beobachtungen zu der Abhandlung von Goldfuss über die Gattung *Archegosaurus*. *Verhandlungen des Naturhistorischen Vereins für Rheinlande und Westphalen* **6:** 76–81.

Laurin M. 2000. Seymouriamorphs. In: Heatwole H, Carroll RL, eds. *Amphibian biology*. Chipping Norton: Surrey Beatty & Sons, 1064–1080.

Laurin M, Girondot M, de Ricqlès A. 2000. Early tetrapod evolution. *Trends in Ecology and Evolution* **15:** 118–123.

Laurin M, Girondot M, Loth MM. 2004. The evolution of long bone microanatomy and lifestyle in lissamphibians. *Paleobiology* **30:** 589–613.

Lebedev OA. 1984. The first find of a Devonian tetrapod vertebrate in the USSR. *Doklady Akademii Nauk SSSR, Palaeontology* **278:** 1470–1473. (in Russian).

Lebedev OA, Clack JA. 1993. Upper Devonian tetrapods from Andreyevka, Tula Region, Russia. *Palaeontology* **36:** 721–734.

Lebedev OA, Coates MI. 1995. The postcranial skeleton of the Devonian tetrapod *Tulerpeton curtum* Lebedev. *Zoological Journal of the Linnean Society* **114:** 307–348.

Levrat-Calviac V, Zylberberg L. 1986. The structure of the osteoderms in the gekko: *Tarentola mauritanica*. *American Journal of Anatomy* **176:** 437–446.

Lucas FA. 1904. A new batrachian and a new reptile from the Triassic of Arizona. *Proceedings of the United States National Museum* **27:** 193–195.

Maddin HC, Musat-Marcu S, Reisz RR. 2007. Histological microstructure of the claws of the African Clawed Frog, *Xenopus laevis* (Anura: Pipidae): implications for the evolution of claws in tetrapods. *Journal of Experimental Zoology (Molecular and Developmental Evolution)* **308B:** 259–268.

Maddison WP, Maddison DR. 2009. Mesquite: a modular system for evolutionary analysis. Version 2.6. Available at http://mesquiteproject.org

Matthes E. 1934. Bau und Funktion der Lippensäume wasserlebender Urodelen. *Zeitschrift für Morphologie und Ökologie der Tiere* **28:** 155–169.

Mehl MG. 1913. A description of *Chenoprosopus milleri* gen. et spec. nov. *Publications of the Carnegie Institution of Washington* **181:** 11–16.

von Meyer H. 1857. Über fossile Saurierknochen des orenburgschen Gouvernements. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* **1857:** 539–543.

von Meyer H. 1858. Reptilien aus der Steinkohlenformation in Deutschland. *Palaeontographica* **6:** 59–219.

von Meyer H, Plieninger T. 1844. *Beiträge zur Paläontologie Württemberg's, enthaltend die fossilen Wirbeltierreste aus den Triasgebilden mit besonderer Rücksicht auf die Labyrinthodonten des Keupers*. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.

Navas CA, Jared C, Antoniazzi MM. 2002. Water economy in the casque-headed tree-frog *Corythomantis greeningi* (Hylidae): role of behaviour, skin, and skull skin co-ossification. *Journal of Zoology* **257:** 525–532.

Pawley K. 2007. The postcranial skeleton of *Trimerorhachis insignis* Cope, 1878 (Temnospondyli: Trimerorhachidae): a plesiomorphic temnospondyl from the Lower Permian of North America. *Journal of Paleontology* **81:** 873–894.

Pawley K, Warren AA. 2006. The appendicular skeleton of *Eryops megacephalus* Cope, 1877 (Temnospondyli: Eryopoidea) from the Lower Permian of North America. *Journal of Paleontology* **80:** 561–580.

Riabinin AN. 1927. *Trematosuchus (?) jakovlevi* nov. sp. from the Lower Triassic deposits in the surroundings of Rybinsk. *Izvestija Geologicheskogo Komiteta (USSR)* **45:** 519–528. (in Russian with English summary).

Riabinin AN. 1930. A labyrinthodont stegocephalian *Wetlugasaurus angustifrons* nov. gen., nov. sp. from the Lower Triassic of Vetluga-Land in northern Russia. *Annales de la Société Paléontologique de Russie* **8:** 49–76. (in Russian).

Romer AS. 1936. Studies on American Permo-Carboniferous tetrapods. *Problems of Paleontology* **1:** 85–93.

Romer AS. 1947. Review of the Labyrinthodontia. *Bulletin of the Museum of Comparative Zoology Harvard College* **99:** 1–368.

Romer AS. 1969. A temnospondylous labyrinthodont from the Lower Carboniferous. *Kirtlandia* **6:** 1–20.

Romer AS. 1972. Skin breathing – primary or secondary? *Respiration Physiology* **14:** 183–192.

Ruta M, Coates MI. 2007. Dates, nodes and character conflict: addressing the lissamphibian origin problem. *Journal of Systematic Paleontology* **5:** 69–122.

Ruta M, Coates MI, Quicke DLJ. 2003. Early tetrapod relationships revisited. *Biological Reviews* **78:** 251–345.

Scheyer TM, Sánchez-Villagra MR. 2007. Carapace bone histology in the giant pleurodiran turtle Stupendemys geographicus: phylogeny and function. *Acta Palaeontologica Polonica* **52:** 137–154.

Schoch RR. 1997a. A new capitosaurid amphibian from the Upper Lettenkeuper (Ladinian) of Kupferzell (Southwestern Germany). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **203:** 239–272.

Schoch RR. 1997b. Cranial anatomy of the Permian temnospondyl amphibian *Zatrachys serratus* Cope 1878, and the phylogenetic position of the Zatracheidae. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **206:** 223–248.

Schoch RR. 2000. The status and osteology of two new cyclotosaurid amphibians from the Upper Moenkopi Formation of Arizona (Amphibia: Temnospondyli; Middle Triassic). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **216:** 387–411.

Schoch RR. 2001. Can metamorphosis be recognised in Palaeozoic amphibians? *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **220:** 335–367.

Schoch RR. 2002. The evolution of metamorphosis in temnospondyls. *Lethaia* **35:** 309–327.

Schoch RR. 2003. Early larval ontogeny of the Permo-Carboniferous temnospondyl *Sclerocephalus*. *Palaeontology* **46:** 1055–1072.

Schoch RR. 2008. A new stereospondyl from the Middle Triassic of Germany, and the origin of the Metoposauridae. *Zoological Journal of the Linnean Society* **152:** 79–113.

Schoch RR. 2009. Evolution of life cycles in early amphibians. *Annual Review of Earth and Planetary Sciences* **37:** 135–162. DOI:10.1146/annurev.earth.031208.100113.

Schoch RR, Carroll RL. 2003. Ontogenetic evidence for the Paleozoic ancestry of salamanders. *Evolution and Development* **5:** 314–324.

Schoch RR, Fröbisch NB. 2006. Metamorphosis and neoteny: alternative developmental pathways in an extinct amphibian clade. *Evolution* **60:** 1467–1475.

Schoch RR, Milner AR. 2000. Stereospondyli. In: Wellnhofer P, ed. *Handbuch der Paläoherpetologie*, Vol. 3B. München: Verlag Dr. Friedrich Pfeil, 1–203.

Schoch RR, Rubidge B. 2005. The amphibamid Micropholis stowii from the Lystrosaurus Assemblage Zone of South Africa. *Journal of Vertebrate Paleontology* **25:** 502–522.

Schoch RR, Witzmann F. 2009a. Osteology and relationships of the temnospondyl genus *Sclerocephalus*. *Zoological Journal of the Linnean Society* **157:** 135–168.

Schoch RR, Witzmann F. 2009b. The temnospondyl *Glanochthon* from the Lower Permian Meisenheim Formation of Germany. *Special Papers in Palaeontology* **81:** 121–136.

Seibert EA, Lillywhite HB, Wassersug RJ. 1974. Cranial co-ossification in frogs: relationship to rate of evaporite water loss. *Physiological Zoology* **47:** 261–265.

Seidel MR. 1979. The osteoderms of the American Alligator and their functional significance. *Herpetologica* **35:** 375–380.

Sennikov AG. 1981. A new wetlugasaur from the Samara River Basin. *Paleontological Journal* **15:** 111–116.

Sequeira SEK. 1998. The cranial morphology and taxonomy of the saurerpetontid *Isodectes obtusus* comb. nov. (Amphibia: Temnospondyli) from the Lower Permian of Texas. *Zoological Journal of the Linnean Society* **122:** 237–259.

Sequeira SEK. 2004. The skull of *Cochleosaurus bohemicus* Frič, a temnospondyl from the Czech Republic (Upper Carboniferous) and cochleosaurid interrelationships. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **94:** 21–43.

Sequeira SEK, Milner AR. 1993. The temnospondyl amphibian *Capetus* from the Upper Carboniferous of the Czech Republic. *Palaeontology* **36:** 657–680.

Shishkin MA, Novikov IV, Gubin YM. 2000. Permian and Triassic temnopsondyls from Russia. In: Benton M, Shishkin MA, Unwin D, Kurochkin E, eds. *The age of dinosaurs in Russia and Mongolia*. Cambridge: Cambridge University Press, 60–70.

Sire JY. 1985. Fibres d'ancrage et couche limitante externe à la surface des écailles du Cichlidae *Hemichromis bimaculatus* (Téléostéen, Perciforme): données ultrastructurales. *Annales des Sciences Naturelles, Zoologie, 13e Série* **7:** 163–180.

Sire JY. 1986. Ontogenic development of surface ornamentation in the scales of *Hemichromis bimaculatus* (Cichlidae). *Journal of Fish Biology* **28:** 713–724.

Smithson TR. 1980. A new labyrinthodont amphibian from the Carboniferous of Scotland. *Palaeontology* **23:** 915–923.

Smithson TR. 1982. The cranial morphology of *Greererpeton burkemorani* Romer (Amphibia: Temnospondyli). *Zoological Journal of the Linnean Society of London* **76:** 29–90.

Steen MC. 1938. On the fossil Amphibia from the gas coal of Nýřany and other deposits in Czechoslovakia. *Proceedings of the Zoological Society London, Series B* **108:** 205–283.

Steyer JS. 2003. A revision of the Early Triassic 'capitosaurs' (Stegocephali, Stereospondyli) from Madagascar, with remarks on their comparative ontogeny. *Journal of Vertebrate Paleontology* **23:** 544–555.

Steyer JS, Laurin M, Castanet J, de Ricqlès A. 2004. First histological and skeletochronological data on temnospondyl growth: palaeoecological and palaeoclimatological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* **206:** 193–201.

Steyer JS, Damiani R, Sidor CA, O'Keefe FR, Larsson HCE, Maga A, Ide O. 2006. The vertebrate fauna of the Upper Permian of Niger. IV. *Nigerpeton ricqlesi* (Temnospondyli: Cochleosauridae), and the edopoid colonization of Gondwana. *Journal of Vertebrate Paleontology* **26:** 18–28.

Sumida SS, Modesto S. 2001. A Phylogenetic Perspective on Locomotory Strategies in Early Amniotes. *American Zoologist* **41:** 586–597.

Trautschold H. 1884. Die Reste permischer Reptilien des Paläontologischen Kabinets der Universität Kasan. *Nouveaux Ménoires de la Société Impériale Des Naturalistes de Moscou* **15:** 1–38.

Trueb L. 1966. Morphology and development of the skull in the frog *Hyla septentrionalis*. *Copeia* **1966:** 562–573.

Trueb L. 1970. Evolutionary relationships of casque-headed tree-frogs with co-ossified skulls (family Hylidae). *University of Kansas Publications Museum of Natural History* **18:** 547–716.

Trueb L. 1973. Bones, frogs, and evolution. In: Vial J, ed. *Evolutionary biology of the anurans*. Columbia: University of Missouri Press, 65–132.

Tverdochlebova GI. 1972. New batrachosaurian genus from the Upper Permian of the southern Cis-Urals. *Paleontologischeskii Zhurnal* **1972:** 95–103. (in Russian).

Vallin G, Laurin M. 2004. Cranial morphology and affinities of *Microbrachis*, and a reappraisal of the phylogeny and lifestyle of the first amphibians. *Journal of Vertebrate Paleontology* **24:** 56–72.

Van Hoepen ECN. 1915. Stegocephalia of Senekal, O. F. S. *Annals of the Transvaal Museum* **5:** 124–149.

Vorobyeva EI, Schultze HP. 1991. Description and systematics of panderichthyid fishes with comments on their relationship to tetrapods. In: Schultze HP, Trueb L, eds. *Origins of the higher groups of tetrapods, controversy and consensus*. Ithaca and London: Comstock Publishing Associates, 68–109.

Warren AA. 2007. New data on *Ossinodus pueri*, a stem tetrapod from the Early Carboniferous of Australia. *Journal of Paleontology* **27:** 850–862.

Warren AA, Marsicano CA. 1998. Revision of the Brachyopidae (Temnospondyli) from the Triassic of Sydney, Carnarvon and Tasmania basins, Australia. *Alcheringa* **22:** 329–342.

Warren AA, Marsicano CA. 2000. A phylogeny of Brachyopoidea (Temnospondyli, Stereospondyli). *Journal of Vertebrate Paleontology* **20:** 462–483.

Watson DMS. 1954. On Bolosaurus and the origin and classification of reptiles. *Bulletin of the Museum of Comparative Zoology* **111:** 297–449.

Watson DMS. 1956. The brachyopid labyrinthodonts. *Bulletin of the British Museum (Natural History) Geology* **2:** 317–391.

Webb JF, Shirey JE. 2003. Postembryonic development of the cranial lateral line canals and neuromasts in zebrafish. *Developmental Dynamics* **228:** 370–385.

Werneburg R. 1991. Die Branchiosaurier aus dem Unterrotliegend des Döhlener Beckens bei. *Dresden. Veröffentlichungen aus dem Naturhistorischen Museum Schleusingen* **6:** 75–99.

Williston SW. 1909. The skull of *Labidosaurus*. *American Journal of Anatomy* **10:** 69–84.

Witzmann F. 2004. The external gills of Palaeozoic amphibians. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **232:** 375–401.

Witzmann F. 2005. Hyobranchial and postcranial ontogeny of the temnospondyl *Onchiodon labyrinthicus* from Niederhäslich (Döhlen Basin, Autunian, Saxony). *Paläontologische Zeitschrift* **79:** 479–492.

Witzmann F. 2006. Cranial anatomy and ontogeny of the Permo-Carboniferous temnospondyl *Archegosaurus decheni* from the Saar-Nahe Basin, Germany. *Transactions of the Royal Society of Edinburgh, Earth Sciences* **96:** 131–162.

Witzmann F. 2007. The evolution of the scalation pattern in temnospondyl amphibians. *Zoological Journal of the Linnean Society* **150:** 815–834.

Witzmann F. In press. Comparative histology of sculptured dermal bones in basal tetrapods, and the implications for the soft tissue dermis. *Palaeodiversity*.

Witzmann F, Pfretzschner HU. 2003. Larval ontogeny of *Micromelerpeton credneri* (Temnospondyli, Dissorophoidea). *Journal of Vertebrate Paleontology* **23:** 750–768.

Witzmann F, Schoch RR. 2006. Skeletal development of the temnospondyl *Acanthostomatops vorax* from the Lower Permian Döhlen basin of Saxony. *Transactions of the Royal Society of Edinburgh, Earth Sciences* **96:** 365–385.

Witzmann F, Scholz H. 2007. Morphometric study of allometric skull growth in the temnospondyl Archegosaurus decheni from the Permian/Carboniferous of Germany. *Geobios* **40:** 541–554.

Witzmann F, Soler-Gijón R. 2008. The bone histology of osteoderms in temnospondyl amphibians and in the chroniosuchian *Bystrowiella*. *Acta Zoologica (Stockholm)* DOI 10.1463–6395.1111/j2008.00385.x

Wyman J. 1858. On some remains of batrachian reptiles discovered in the coal formation of Ohio, by Dr. J. S. Newberry and C. M. Wheatley. *American Journal of Science* **25:** 158–163.

Yates AM, Warren AA. 2000. The phylogeny of the 'higher' temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. *Zoological Journal of the Linnean Society* **128:** 77–121.

Zhu M, Schultze HP. 2001. Interrelationship of basal osteichthyans. In: Ahlberg P, ed. *Major events in vertebrate evolution*. London: Taylor & Francis, 289–314.

Zittel KA. 1911. *Grundzüge der Paläontologie (Paläozoologie). II. Abteilung. Vertebrata*, Second edn. München and Berlin: Verlag von R. Oldenbourg.

Zylberberg L, Castanet J. 1985. New data on the structure and the growth of the osteoderms in the reptile *Anguis fragilis* L. (Anguidae, Squamata). *Journal of Morphology* **186:** 327–342.

APPENDIX 1

OUTER SCULPTURAL MORPHOLOGY HAS BEEN STUDIED IN THE FOLLOWING TAXA (*INDICATES THAT THIN SECTIONS HAVE BEEN PREPARED FROM THE RESPECTIVE SPECIMEN)

Taxon	Stratigraphy	Locality	Specimens/Remarks
Stem tetrapods			
Panderichthys rhombolepis (Gross, 1930)	Late Devonian, Gauja beds	Latvia	PIN 2846/2, complete skull; MB.f.17548, dermal skull fragments
Acanthostega gunnari Jarvik, 1952	Late Devonian, upper Famennian, Britta Dal Fm.	Stensiö Bjerg, Greenland	MGUH f.n. 1300b, complete skull
Ventastega curonica Ahlberg *et al.*, 1994	Late Devonian, upper Famennian, Ketleri Fm.	Venta River, Ketleri, Latvia	PIN 54/180, premaxilla; 1491/82, left suspensorium; 1491/85, fragment of angular
Ichthyostega sp.	Late Devonian, upper Famennian, Britta Dal Fm.	Sederholm Bjerg, Greenland	SMNS without number (cast of MGUH A.71), nearly complete skull
?Tulerpeton curtum[1] Lebedev, 1984	Late Devonian, Famennian	Andreyevka-2 locality, Tula Region, Central Russia	PIN 2921/8, right premaxilla; 2921/31, right angular; 2921/39, parietal; 2921/40, supratemporal; 2921/41, right postfrontal; 2921/3002, postparietal; 2921/3003, intertemporal
Megalocephalus pachycephalus (Barkas, 1873)	Late Carboniferous, Westphalian A, Betterbed Coal	Low Moor Horizon, Yorkshire, UK	MCZ 6979, lower jaw symphysis
Temnospondyls			
Edops craigi Romer, 1936	Early Permian	Terapin School, Archer County, Texas, USA	MCZ 1378, complete skull with lower jaws; 1235, several fragments of dermal skull roof
Chenoprosopus milleri Mehl, 1913	Early Permian, Cutler Fm.	New Mexico, USA	UCMP 41104*, fragments of dermal skull roof
Cochleosaurus bohemicus (Frič, 1876)	Late Carboniferous, Westphalian D, Gaskohle	Nýřany, Czech Republic	MB.Am.80, complete skull
Trimerorhachis insignis Cope, 1878	Early Permian	Archer County, Texas, USA	MCZ 1168, complete skull; 1169, fragment of skull table; 2401, lower jaw; 3221, complete skull; 8286, posterior part of skull table; 8287, supratemporals; 8398, isolated jugals
Dvinosaurus primus Amalitzky, 1921	Late Permian, Upper Tatarian	Sokolki, North Dvina River, Russia	PIN 156/10, almost complete skull
Isodectes obtusus[2] (Cope, 1868)	Late Carboniferous (AMNH 11037), Early Permian (AMNH 2455)	Linton, Ohio, USA (AMNH 11037); ?Clear Fork Gr., Texas, USA (AMNH 2455)	AMNH 11037, cast of skull and anterior body; 2455, almost complete skull
Capetus palustris Steen, 1938	Late Carboniferous, Westphalian D, Gaskohle	Nýřany, Czech Republic	MB.Am.84, almost complete skull

APPENDIX 1 *Continued*

Taxon	Stratigraphy	Locality	Specimens/Remarks
Sclerocephalus haeuseri Goldfuss, 1847	Early Permian, Autunian, Jeckenbach Black Shale Horizon	Heimkirchen, Saar-Nahe Basin, Germany	SMNS 90507, cast of neotype, almost complete skull with trunk
Cheliderpeton latirostre (Jordan, 1849)	Early Permian, Autunian, Humberg Black Shale	Saar-Nahe Basin, Germany	SMNS 91003, skull with complete postcranium
Platyoposaurus stuckenbergi (Trautschold, 1884)	Late Permian, Upper Kazanian	Belebey, Bashkortostan	PIN 3968/1, cast of complete skull; PIN uncatalogued, snout with mandible; 49/19, symphysis of lower jaw; 49/28 and 161/51, clavicular blades
Melosaurus uralensis von Meyer, 1857	Late Permian	Kazanian, Sterlitamak, Bashkortostan	PIN 161/1, complete skull; 161/2, fragment of snout; 161/3, symphysis of lower jaw; 683/1, lower jaw
Benthosuchus sushkini (Efremov, 1929)	Early Triassic, Rybinskian Horizon, Vetluga Series	Sharzenga River, Vologodska Region, Russia	PIN 2-19-2252, complete skull
Wetlugasaurus angustifrons Riabinin, 1930 (*Volgosuchus cornutus*)	Early Triassic, Sludkian Horizon	Vetluga River, Niznhii Novgorod Province, Russia	PIN 155/2, posterior portion of skull
Wetlugasaurus samarensis Sennikov, 1981	Early Triassic, Kopanskaya Svita, Vokhmian Horizon	Samara River Basin, Orenburg Province, Russia	PIN 4627/1, almost complete skull
Thoosuchus jakovlevi (Riabinin, 1927)	Early Triassic, Smithian, Rybinskian and Sludkian Horizons, Vetluga Series	Rybinsk Region, Russia	SMNS 80064, skull without snout region
Callistomordax kugleri Schoch, 2008	Middle Triassic, Upper Ladinian, Lower Keuper, Erfurt Fm.	Vellberg, Baden-Württemberg, Germany	SMNS 55385, complete skull
Metoposaurus fraasi Lucas, 1904	Late Triassic, Chinle Fm.	Apache County, Arizona, USA	UCMP 27103, complete set of bones of a dermal skull roof; 26711, interclavicle; 27058, clavicular blade; UCMP uncatalogued, clavicular blade
Mastodonsaurus giganteus (Jaeger, 1828)	Middle Triassic, Ladinian, Lettenkeuper	Baden-Württemberg, Germany	SMNS 80878, broken parts of a complete skull; 80889, 80890, SMNS without number, complete skull; 54675, cast of complete skull; SMNS without number*, several dermal bone fragments; MB.Am.1434, clavicle
Eocyclotosaurus wellesi Schoch, 2000	Middle Triassic, Anton Chico Mb., Moenkopi Fm.	New Mexico, USA	SMNS 90061, posterior part of skull with skull table and cheek

APPENDIX 1 *Continued*

Taxon	Stratigraphy	Locality	Specimens/Remarks
Cyclotosaurus robustus (von Meyer & Plieninger, 1844)	Late Triassic, Upper Carnian, Schilfsandstein	Baden-Württemberg, Germany	SMNS 4139, right half of a skull; 5775, complete skull
Kupferzellia wildi Schoch, 1997b	Middle Triassic, Upper Ladinian, Upper Lettenkeuper	Baden-Württemberg, Germany	SMNS 54671, several fragments of dermal skull roof and palate
Vigilius wellesi Warren & Marsicano, 2000	Early Triassic	Holbrook Quarry, Navajo County, Arizona, USA	ROM 23857, complete skull, cast of holotype
Plagiosuchus pustuliferus (Fraas, 1896)	Middle Triassic, Ladinian, Lettenkeuper	Baden-Württemberg, Germany	SMNS 57921, complete skull with mandible
Gerrothorax pulcherrimus (Fraas, 1913)	Late Triassic, Norian, Middle Stubensandstein	Baden-Württemberg, Germany	SMNS 12592, complete skull
Gerrothorax pustuloglomeratus (von Huene, 1922)	Middle Triassic, Ladinian, Longobardian	Baden-Württemberg, Germany	SMNS 83866, complete specimen; 84788, skull roof; SMNS without number, interclavicle, several osteoderms
Plagiosternum granulosum (Fraas, 1889)	Middle Triassic, Ladinian, Grenzbonebed	Baden-Württemberg, Germany	SMNS 13168, posterior part of skull; 56614, complete skull; SMNS without number, clavicle; SMNS without number*, interclavicle
Eryops megacephalus Cope, 1877	Early Permian, Moran Fm., Wichita Group	Little Bitter Creek, Young County, Texas, USA	MCZ 1790, several dermal bone fragments; 1792, two premaxillae; 1793, snout; 1852, fragments of dermal skull roof and mandible; 1914, complete skull; 2691, snout; 2696, posterior part of mandible; 2728, maxilla; 3233, complete skull; 7330, fragment of skull table; 7697, angular and dentary
Acanthostomatops vorax (Credner, 1883)	Early Permian, Autunian	Döhlen Basin, Saxony, Germany	LFUG-13245, complete skull with vertebral column
Zatrachys serratus Cope, 1878	Early Permian, Cutler Fm.	Welles Quarry, Rio Arriba County, New Mexico, USA	UCMP 34154, 34179, 34178, 34157, 34158, complete skulls; 34159, 34156, left half of skull table plus cheek; 34161, right half of snout
Amphibamus lyelli Wyman, 1858	Late Carboniferous	Jefferson County, Linton, Ohio, USA	MB.Am.331, complete skull
Broiliellus sp.	Early Permian, Putnam Fm., Wichita Group	Archer County, Texas, USA	MCZ 1694, several fragments of the dermal skull roof
Dissorophus multicinctus Cope, 1895a	Early Permian, Arroyo Fm.	Willbarger and Baylor Counties, Texas, USA	MCZ 4179, part of the skull; 4174, 4193, posterior part of mandible

APPENDIX 1 *Continued*

Taxon	Stratigraphy	Locality	Specimens/Remarks
Platyhystrix rugosus Case, 1910	Early Permian, Cutler Fm.	Welles Quarry loc., New Mexico, USA	UCMP 39090, 39092, fragments of skull roof
Kamacops acervalis Gubin, 1980	Late Permian, Upper Kazanian, Belebey Fm.	Yerzovka, Perm province, Russia	PIN 3817/1, squamosal plus tabular; 554/333, complete skull; 1758/332, several pieces of dermal skull
Iratusaurus vorax Gubin, 1980	Late Permian, Upper Kazanian, Belebey Fm.	Belebey, Bashkortostan	PIN 164/300, left part of skull table with cheek and orbital region
Phonerpeton pricei Dilkes, 1990	Early Permian, Putnam Fm., Wichita Group	Archer County, Texas, USA	AMNH 7150, complete skull
Micropholis stowi Huxley, 1859	Early Triassic, *Lystrosaurus* Zone, Beaufort Fm.	Wonderkrantz, Harrismith District, Orange Free State Province, South Africa	UCMP 173220, skull plus parts of pectoral girdle
Lepospondyls			
Diplocaulus magnicornis Cope, 1882	Early Permian, Arroyo Fm.	Texas, USA	MCZ 1187, lateral 'horn'; 1188, 1189, almost complete skulls; 1247, skull with mandible; 1254, 1255, several dermal skull fragments; 1964, almost complete skull
Embolomeri			
Archeria crassidisca Cope, 1884	Early Permian, Geraldine Bonebed	Geraldine, Texas, USA	MCZ 2045, complete skull; 2049, 2051, 2063, 2072, 2121, almost complete skulls; 2947, right part of skull
Chroniosuchia			
Chroniosaurus dongusensis Tverdochlebova, 1972	Late Permian, Upper Tatarian, Malokinel'skaya Svita Horizon	Donguz River, Ural Basin, Orenburg Province, Russia	PIN 3713/11, 3713/38, isolated skull tables; 3713/14, cheek that belongs to 3713/38; 3595/124, juvenile skull with vertebral column plus osteoderms
Seymouriamorpha			
Seymouria baylorensis Broili, 1904	Early Permian	Baylor County, Clear Fork, West Coffee Creek, Texas, USA	MCZ 1081, complete skull; 1083, almost complete skull; 1084, posterior skull table; 1086, several fragments of skull
Parareptilia			
Lanthanosuchus watsoni Efremov, 1946	Late Permian, Lower Tatarian	Isheyevo village, Republic of Tatarstan, Russia	PIN 271/1, complete skull; 157/97, 88, 1058, fragments of dermal skull
Lanthaniscus efremova Ivakhnenko, 1980	Late Permian, upper Kazan	Mezen River Basin, Pezo River, Archangel Province, Russia	PIN 3706/9, skull with vertebral column, pectoral girdle and parts of the limbs

APPENDIX 1 *Continued*

Taxon	Stratigraphy	Locality	Specimens/Remarks
Eureptilia			
Captorhinus aguti (Cope, 1882)	Early Permian	Dolese Quarry, Oklahoma, USA	MCZ without number*, several fragments of dermal skull roof
Captorhinus (*Eocaptorhinus*) *laticeps* (Williston, 1909)	Early Permian, Artinskian, Upper Wichita Group, Upper Belle Plains Fm.	Texas, USA	MCZ 1483, squamosal
Labidosaurus hamatus Cope, 1895b	Early Permian, Artinskian, Clear Fork Group	Texas, USA	MCZ 8123, several fragments of dermal skull roof; 8724, fragment of dermal skull roof; 8727, fragments of frontal, parietal, and postorbital; MCZ without number, numerous fragments of dermal skull

[1]With the exception of PIN 2921/8, the referred tetrapod material from this locality cannot unambiguosly be assigned to *Tulerpeton curtum*, although this is most likely (Lebedev & Clack, 1993).
[2]AMNH 2455 is the holotype of *Eobrachyops townendae* Watson, 1956 that was identified as *I. obtusus* by Sequeira (1998).

APPENDIX 2

1. The sculptural ridges differ conspicuously in their height, higher and lower ridges are randomly distributed on each bone (1); the height of the sculptural ridges is mostly constant on each bone (2).
2. The width of the sculptural ridges differs conspicuously on each bone (1); the width of the ridges is approximately constant on each bone (2).
3. The ridges between the nodal points reach mostly the height of the nodal points, or are slightly lower (1); regions are present on which the ridges reach approximately the height of the nodal points as well as regions on which they are lower than the nodal points (2); most ridges are conspicously lower than the nodal points (3).
4. The ridges of most cells have at least half the width of the diameter of the appertaining cell (1); regions are present in which the ridges have at least half the width of the diameter of the appertaining cells and regions, in which the width is less than half the diameter (2); the ridges of most cells are narrower than half the diameter of the appertaining cell (3).
5. The nodal points are not or only slightly broadened with respect to the ridges (1); the nodal points are often distinctly broadened with respect to the ridges (2).
6. Dominating sculptural ridges are absent (1); dominating sculptural ridges are present* (2).

*These are pronounced ridges that run over a long distance and on more than one bone, from nodal point to nodal point.

7. The sculptural ridges are broadly rounded dorsally (1); some ridges are broadly rounded dorsally, others are narrow or edged dorsally (2); ridges are narrow or edged dorsally (3).
8. Regions with distinctly subdued sculpture or without sculpture are present (1); sculpture is present on all cranial dermal bones (2).
9. Sculptural cells consitute most of the sculptural pattern (1); radiating ridges and furrows constitute most of the sculptural pattern (2).
10. The sculptural cells are rather hexagonal in outline (1); both hexagonal and rounded cells are present (2); the sculptural cells are rather rounded in outline (3).
11. The lateral line system is enclosed in bone or partially enclosed in bone, thereby opening via pores to the surface, and may partially course in sulci that are deeply incised, with rather smooth walls (1); lateral line system left weak, discontinuous furrows on the dermal sculpture (2); lateral line system left deep sulci that are continuous or consist of longer sections (3); no imprints of lateral line sulci or pores visible ('external absence' of sulci and pores) (4).
12. No nodal points are pronounced and form tubercles (1); many nodal points are pronounced and form tubercles (2).

APPENDIX 3

	Character states of the 12 variables											
Taxon	1	2	3	4	5	6	7	8	9	10	11	12
Panderichthys	1	1	3	2	2	1	1	2	1	3	1	2
Ichthyostega	1	1	3	2	2	1	1	2	1	2	1	2
Tulerpeton	1	1	1	2	1	1	1	1	1	3	1	1
Acanthostega	1	2	2	3	1	1	2	2	1	2	1	1
Greererpeton	2	2	1	3	2	1	3	2	1	3	1	1
Edops	1	1	2	3	1	1	3	2	1	1	4	1
Cochleosaurus	1	1	1	2	1	1	2	1	1	2	4	1
Trimerorhachis	2	2	1	3	1	1	1	2	1	2	3	1
Dvinosaurus	2	2	2	3	1	1	1	2	2	1	3	1
Isodectes	2	2	2	3	1	1	1	2	1	2	3	1
Capetus	1	1	2	3	1	1	2	1	1	1	4	1
Sclerocephalus	1	1	1	3	1	1	2	2	1	1	2	1
Cheliderpeton	1	1	1	3	1	1	2	2	1	1	2	1
Platyoposaurus	2	2	1	3	1	1	1	2	1	1	2	1
Melosaurus	2	1	1	2	1	1	1	2	1	1	2	1
Plagiosuchus	1	1	2	1	2	1	1	1	2	3	3	2
Plagiosternum	1	2	3	2	2	1	1	1	1	2	3	2
Gerrothorax	1	1	3	2	2	1	1	2	1	3	3	2
Vigilius	1	1	2	3	1	1	2	1	2	1	3	1
Benthosuchus	2	2	2	3	1	1	1	2	1	1	3	1
Wetlugasaurus	1	2	3	3	1	1	1	2	1	1	2	1
W. angustifrons	2	2	1	3	1	1	1	2	1	1	3	1
Thoosuchus	1	2	2	3	1	1	1	2	2	1	3	1
Callistomordax	2	2	1	3	1	1	1	2	1	1	2	1
Metoposaurus	2	2	1	3	1	1	1	2	1	1	3	1
Mastodonsaurus	1	2	2	3	1	1	1	2	1	1	3	1
Eocyclotosaurus	2	2	1	3	1	1	2	2	1	1	3	1
Cyclotosaurus	2	2	1	3	1	1	1	2	1	1	3	1
Kupferzellia	2	2	2	3	1	1	1	2	1	1	3	1
Eryops	1	1	2	3	1	1	2	2	1	2	4	1
Acanthostomatops	1	1	3	3	2	2	2	2	1	2	4	2
Zatrachys	1	1	3	2	2	2	2	1	2	3	4	2
Broiliellus	1	1	1	2	1	1	1	2	1	3	4	1
Amphibamus	1	2	3	3	2	1	1	1	2	3	4	1
Platyhystrix	1	1	3	1	2	1	1	2	1	3	4	2
Kamacops	1	1	2	2	2	1	1	2	1	3	4	2
Micropholis	1	1	3	2	2	1	1	2	1	3	4	2
Phonerpeton	1	2	2	3	1	1	2	2	1	2	4	1
Chroniosaurus	1	1	3	2	2	2	1	2	1	3	4	2
Archeria	1	1	1	2	1	1	2	1	2	3	3	1
Seymouria	1	2	3	2	1	1	1	2	1	1	4	1
Diplocaulus	2	2	1	3	1	1	1	2	1	3	2	1
Lanthaniscus	1	1	3	3	2	2	1	2	2	2	4	2
Lanthanosuchus	1	1	3	2	2	2	1	2	1	3	4	2
Labidosaurus	2	2	1	2	1	1	1	2	1	2	4	1
Captorhinus aguti	2	2	1	3	1	1	1	2	1	1	4	1
Captorhinus laticeps	2	2	1	3	1	1	1	2	1	3	4	1

APPENDIX 4

TAXA OF BASAL TETRAPODS CONSIDERED FOR PRINCIPAL COMPONENT ANALYSIS (PCA), AND THEIR PRESUMED LIFESTYLE

Taxon	Adult lifestyle; morphological criteria (references)
Panderichthys rhombolepis (Gross, 1930)	Aquatic; lateral lines, presence of fins (Vorobyeva & Schultze, 1991)
Acanthostega gunnari Jarvik, 1952	Aquatic; lateral lines, gill skeleton, paddle-like limbs (Clack, 2000)
?*Tulerpeton curtum* Lebedev, 1984	Aquatic; lateral lines (Lebedev & Clack, 1993)
Greererpeton burkemorani Romer, 1969	Aquatic; lateral lines (Smithson, 1982), postbranchial lamina (Lebedev & Coates, 1995)
Edops craigi Romer, 1936	?Semi-terrestrial; no lateral line sulci, well-ossified postcranium (Schoch, 2002)
Cochleosaurus bohemicus (Frič, 1876)	?Semi-terrestrial; no lateral line sulci (Schoch, 2009)
Trimerorhachis insignis Cope, 1878	Aquatic; lateral lines, gill skeleton, branchial dentition (Schoch, 2002), poorly ossified postcranium (Pawley, 2007)
Dvinosaurus primus Amalitzky, 1921	Aquatic; lateral lines, gill skeleton (Bystrow, 1938)
Isodectes obtusus (Cope, 1868)	Aquatic; lateral lines (Sequeira, 1998), branchial dentition (FW, pers. observ.)
Capetus palustris Steen, 1938	?Semi-terrestrial; no lateral line sulci, postcranium unknown (Sequeira & Milner, 1993)
Scleroccphalus haeuseri Goldfuss, 1847	Aquatic; lateral lines, long swimming tail (Schoch, 2002)
Cheliderpeton latirostre (Jordan, 1849)	Aquatic; lateral lines, poorly ossified postcranium (Boy, 1993)
Platyoposaurus stuckenbergi (Trautschold, 1884)	Aquatic; lateral lines (Bystrow, 1935; Shishkin, Novikov & Gubin, 2000)
Melosaurus uralensis von Meyer, 1857	Aquatic; lateral lines (FW, pers. observ.)
Benthosuchus sushkini (Efremov, 1929)	Aquatic; lateral lines (Bystrow, 1935)
Wetlugasaurus angustifrons Riabinin, 1930	Aquatic; lateral lines (Schoch & Milner, 2000)
Wetlugasaurus samarensis Sennikov, 1981	Aquatic; lateral lines (Sennikov, 1981)
Thoosuchus jakovlevi (Riabinin, 1927)	Aquatic; lateral lines (Schoch & Milner, 2000)
Callistomordax kugleri Schoch, 2008	Aquatic; lateral lines, branchial ossicles, feeble limbs (Schoch, 2008)
Metoposaurus fraasi Lucas, 1904	Aquatic lifestyle in metoposaurids is indicated by lateral lines, small limbs (Schoch & Milner, 2000) and bone histology (Steyer *et al.*, 2004)
Mastodonsaurus giganteus (Jaeger, 1828)	Aquatic; lateral lines, poorly ossified limbs (Schoch & Milner, 2000)
Eocyclotosaurus wellesi Schoch, 2000	Aquatic; lateral lines (Schoch, 2000)
Cyclotosaurus robustus (von Meyer & Plieninger, 1844)	Aquatic; lateral lines (Schoch & Milner, 2000)
Kupferzellia wildi Schoch, 1997a)	Aquatic; lateral lines (Schoch, 1997a)
Vigilius wellesi Warren & Marsicano, 2000	Aquatic; lateral lines (Warren & Marsicano, 2000)
Plagiosuchus pustuliferus (Fraas, 1896)	Aquatic; lateral lines, gill skeleton (Damiani *et al.*, 2009)
Gerrothorax pustuloglomeratus (von Huene, 1922)	Aquatic; lateral lines, gill skeleton, branchial chamber, small limbs; (Hellrung, 2003)
Plagiosternum granulosum (Fraas, 1889)	Aquatic; lateral lines (Gastou, 2007)
Eryops megacephalus Cope, 1877	Semi-terrestrial; no lateral line sulci, aquatic feeding (Schoch, 2002; Schoch, 2009), massive, large limbs, well-ossified postcranium (Pawley & Warren, 2006)
Acanthostomatops vorax (Credner, 1883)	Terrestrial; no lateral line sulci, well differentiated limbs, terrestrial feeding (Witzmann & Schoch, 2006)
Zatrachys serratus Cope, 1878	Terrestrial; no lateral line sulci, terrestrial feeding (Schoch, 1997b)

APPENDIX 4 *Continued*

Taxon	Adult lifestyle; morphological criteria (references)
Amphibamus lyelli Wyman, 1858	Terrestrial; no lateral line sulci, long, slender limbs (Carroll, 1964)
Broiliellus sp.	Terrestrial; no lateral line sulci, well ossified girdles and limbs (Carroll, 1964)
Dissorophus multicinctus Cope, 1895a	Terrestrial; no lateral line sulci, well-ossified girdles and limbs; (DeMar, 1968)
Platyhystrix rugosus Case, 1910	Terrestrial; no lateral lines (Berman, Reisz & Fracasso, 1981)
Kamacops acervalis Gubin, 1980	?Terrestrial; no lateral line sulci (Gubin, 1980), postcranium unknown
Phonerpeton pricei Dilkes, 1990	Terrestrial; no lateral line sulci, well-differentiated limbs (Dilkes, 1990)
Micropholis stowi Huxley, 1859	Terrestrial; no lateral line sulci, well-differentiated limbs (Schoch & Rubidge, 2005)
Diplocaulus magnicornis Cope, 1882	Aquatic; lateral lines, feeble limbs, long, deep swimming tail (Bossy & Milner, 1998)
Archeria crassidisca Cope, 1884	Semiterrestrial; lateral lines, well-developed limbs (Holmes, 1989)
Chroniosaurus dongusensis Tverdochlebova, 1972	Terrestrial or semi-terrestrial; no lateral line sulci, dorsal osteoderms reinforced vertebral column, microstructure of long bones (Laurin *et al.*, 2004)
Seymouria baylorensis Broili, 1904	Terrestrial; no lateral lines, fully ossified postcranium and large, robust limbs (Laurin, 2000)
Lanthanosuchus watsoni Efremov, 1946	Mode of life not clear; aquatic lifestyle suggested by flattened skull (Watson, 1954); terrestrial lifestyle suggested by slender limbs (Ivakhnenko, 1980)
Lanthaniscus efremova Ivakhnenko, 1980	See *Lanthanosuchus*
Captorhinus aguti (Cope, 1882)	Terrestrial; robust axial and appendicular skeleton (Sumida & Modesto, 2001)
Captorhinus (*Eocaptorhinus*) *laticeps* (Williston, 1909)	Terrestrial; see *Captorhinus aguti*
Labidosaurus hamatus Cope 1895b	Terrestrial; see *Captorhinus aguti*

Dermal bone sculpture in early tetrapods: external morphology, histology and possible functions

Appendix 2

Witzmann, F. 2009. Comparative histology of sculptured dermal bones in basal tetrapods, and the implications for the soft tissue dermis. – Palaeodiversity 2: 233–270.

Palaeodiversity 2: 233 270; Stuttgart, 30.12.2009.

Comparative histology of sculptured dermal bones in basal tetrapods, and the implications for the soft tissue dermis

Florian Witzmann

Abstract

The histology of the sculptured dermal bones of skull and pectoral girdle of 19 taxa of Palaeozoic and Mesozoic basal tetrapods and of the porolepiform *Laccognathus* is investigated. The dermal bones consist generally of compact external and internal cortices that frame a cancellous or trabecular middle region. In *Laccognathus*, thin, unmineralized Sharpey's fibers that are loosely arranged penetrate the external cortex between the odontodes. After the reduction of odontodes in finned stem-tetrapods, dermal sculpture developed via preferential growth of bone without the involvement of resorptive processes. In the stem-tetrapod *Panderichthys*, the Sharpey's fibers are well-mineralized and indicate a tight connection to the overlying soft-tissue integument. The fibers are most numerous and most densely arranged in the bony ridges and tubercles, which constituted the main points of anchorage for the skin. The morphology and morphogenesis of the bony sculpture and its association with mineralized Sharpey's fibers was retained during the fish-tetrapod transition and basically conserved in the different lineages of basal tetrapods including basal amniotes.

The dermal bones of the stem-tetrapods *Panderichthys*, *Acanthostega* and *Greererpeton* are composed to a large degree of parallel-fibered bone, and a 'fish-like' character is the internal cortex that consists of isopedine. In crown-group tetrapods, the Sharpey's fibers are generally much thicker and more densely arranged than in stem-tetrapods, and metaplastic bone can be demonstrated in addition to parallel-fibered bone in many taxa. These data suggest that the first crown-group tetrapods had attained a denser integument that might have provided a better resistance against water loss and mechanical damage during locomotion on land. In contrast to extant lissamphibians, the denser integument as well as ossified dermal scales and the comparatively large body size probably precluded large-scale cutaneous respiration in most basal tetrapods.

The middle region of dermal bones shows varying degrees of resorption and secondary growth among taxa. In heavily ossified forms such as *Eryops* or *Mastodonsaurus*, the weight of the skeleton helped them to stay under water, whereas skeletal lightening by reduced cortices and a highly porous middle region may have enhanced the agility and manoeuvrability during swimming.

Keywords: Bone microstructure, fish-tetrapod transition, integument, Mesozoic, metaplasia, Palaeozoic, Sharpey's fibers.

Zusammenfassung

In dieser Studie wird die Histologie der skulptierten Hautknochen des Schädels und des Schultergürtel von 19 Taxa basaler Tetrapoden aus dem Paläozoikum und Mesozoikum sowie des Porolepiformen *Laccognathus* untersucht. Die Hautknochen bestehen normalerweise aus kompakten äußeren und inneren Cortices, die eine spongiöse mittlere Region einschließen. *Laccognathus* besitzt dünne, nicht mineralisierte Sharpey'sche Fasern im externen Cortex, die locker zwischen den Odontoden angeordnet sind. Nach Reduktion der Odontoden bei fischartigen Stamm-Tetrapoden entstand die äußere Skulptur der Dermalknochen durch bevorzugtes Knochenwachstum ohne Anzeichen damit verbundener Knochenresorption. Bei dem Stamm-Tetrapoden *Panderichthys* sind die Sharpey'schen Fasern gut mineralisiert und deuten auf eine feste Verbindung zwischen der Knochenoberfläche und der überlagernden Haut hin. Die Fasern sind am zahlreichsten und dichtesten in den knöchernen Tuberkeln und Leisten angeordnet, welche die Hauptverankerungspunkte der Haut darstellten. Morphologie und Morphogenese der Knochenskulptur und ihre Assoziation mit mineralisierten Sharpey'schen Fasern wurden während des Fisch-Tetrapoden Überganges beibehalten und in den verschiedenen Linien basaler Tetrapoden einschließlich basaler Amnioten bewahrt.

Die Hautknochen der Stamm-Tetrapoden *Panderichthys*, *Acanthostega* und *Greererpeton* bestehen zu einem großen Teil aus parallelfaserigem Knochen, und ein „fischartiges" Merkmal ist das Vorhandensein von Isopedin im internen Cortex. Bei Kronengruppen-Tetrapoden sind die Sharpey'schen Fasern im allgemeinen deutlich dicker und dichter angeordnet als bei Stamm-Tetrapoden, und neben parallelfaserigem Knochen kann oft metaplastischer Knochen nachgewiesen werden. Diese Befunde deuten darauf hin, dass die ersten Kronengruppen-Tetrapoden eine derbe Haut besessen haben, die wahrscheinlich einen besseren Schutz gegen Wasserverlust und Verletzung beim Laufen über das Land bot. Im Gegensatz zu heutigen Lissamphibien verhinderten die derbere Haut sowie die häufig vorhandenen Knochenschuppen und das ungünstige Verhältnis von Körperoberfläche zu Volumen eine weitreichende Hautatmung bei den meisten basalen Tetrapoden.

Die mittlere Region der Hautknochen war von Taxon zu Taxon in unterschiedlichem Maße von Resorption und sekundärem Wachstum betroffen. Bei schwer verknöcherten Formen wie *Eryops* und *Mastodonsaurus* wirkte das Gewicht des Skeletts dem Auftrieb im Wasser entgegen, wohingegen eine Gewichtsreduktion durch dünnere Cortices und eine stark poröse mittlere Region die Wendigkeit beim Schwimmen sicherlich erhöht hat.

Contents

1. Introduction

Dermal bones of the skull and the pectoral girdle develop within the integument, generally in the lower layer of the dermis (Castanet et al. 2003). These ossifications are frequently penetrated by numerous canals that carried blood vessels and nerves (including the lateral line system of fishes and non-amniote basal tetrapods) to the external bone surface and into the directly overlying integument. The histomorphology of dermal bones as well as the structure of their external surface are therefore well suited as osteological correlates of the integumentary structure in fossil vertebrates. In the different groups of fossil fishes and early vertebrates, the dermal bones of skull and pectoral girdle, the scales and armour plates have been subject to histological investigation for a long time, so that the internal structure of these dermal ossifications are the most extensively studied among vertebrates (e. g., Bystrow 1939, 1942, 1957; Ørvig 1951, 1957, 1966, 1968, 1989; Thomson 1977; Gross 1930, 1957, 1973; Bemis & Northcutt 1992; Smith 1977).

In fossil tetrapods, the focus of histological investigations lies most often on the long bones, including the application of skeletochronology as an important method to infer biological parameters like growth rate, individual age and mode of life, and a large amount of data has accumulated over the last decades (e. g., de Ricqlès 1975a, b, 1976, 1977, 1981, 1993; Chinsamy 1993; Chinsamy-Turan 2005; Damiani 2000; Steyer et al. 2004; Sander & Andrássy 2006; Klein & Sander 2007, 2008; Sanchez et al. 2008). More recently, also the histology of dermal ossifications of the trunk (i. e., osteoderms) in fossil amniotes

has attracted increasing interest of palaeontologists and zoologists, e. g. in turtles (SCHEYER & SÁNCHEZ-VILLAGRA 2007; SCHEYER & ANQUETIN 2008), placodonts (SCHEYER 2007), dinosaurs (DE BUFFRÉNIL et al. 1986; DE RICQLÈS et al. 2001; SCHEYER & SANDER 2004; MAIN et al. 2005), xenarthrans (HILL 2005, 2006), and basal tetrapods (WITZMANN & SOLER-GIJÓN 2008).

The histology of the dermal ossifications of skull and pectoral girdle in temnospondyls and other basal tetrapods, in contrast, has received the attention of comparatively few workers who investigated only a very limited range of taxa. Within the work on the Early Permian 'branchiosaurs' from the Döhlen Basin in Saxony, CREDNER (1893, pl. 30, figs. 4–6; pl. 31, figs. 8–9) illustrated schematically the course of presumed blood vessels in dermal skull bones of the temnospondyl *Onchiodon* and presented a histological section of the vomer (CREDNER 1893, pl. 31, fig. 4).

SEITZ (1907) described the histology of a mandible fragment of ?*Mastodonsaurus*. He observed a compact outer region consisting of lamellar bone with simple vascular canals and primary osteons. More internally in the bone, SEITZ (1907) found secondary osteons (Haversian systems) and irregular caverns of a spongy region.

GROSS (1934) provided a short description of the dermal skull bone histology of *Mastodonsaurus*, *Metoposaurus* and *Plagiosternum*. He recognized that the dermal bones of these temnospondyls exhibit a diploë structure, i. e., a spongy middle region is framed by an external and an internal compact cortex, and designated the matrix of the cortical bone as zonal periosteal bone (zonarer Periostknochen).

As GROSS (1934) noted, the internal cortex lacks the isopedine-like organization of many finned sarcopterygians. A detailed study of the histology of dermal skull bones in the stereospondyl *Benthosuchus* was published by BYSTROW (1935). He recognized horizontally aligned large canals in the middle, spongy region from which oblique canals branch off, traverse the external cortex and open to the external bone surface on the floor of the sculptural pits and furrows. BYSTROW (1935) described a fine network of capillaries additional to these large canals in the external region that open to the bone surface via small pores. He designated this network as 'rete vasculosum'. In a later study, BYSTROW (1947) interpreted these capillaries as serving for cutaneous respiration and compared the vascularization of the dermal bones of *Benthosuchus* with those of the stereospondylomorphs *Wetlugasaurus* and *Platyoposaurus*, and the dvinosaur *Dvinosaurus*. In his studies, BYSTROW (1935, 1947) had focused mainly on the morphology and course of blood vessels within the bone, but he neither described the bone matrix proper nor the presence of extrinsic fibers.

In the first part of their comprehensive works on bone histology, ENLOW & BROWN (1956) concentrated on the study of long bones of tetrapods, but also commented on the arrangement and orientation of vascular canals in dermal bones of temnospondyls (*Edops*, *Trimerorhachis*, *Eryops*) and of the stem-amniote *Seymouria*. PEABODY (1961) investigated cyclical growth zones in sections of the dentaries of Early Permian 'microsaurs' and indeterminate 'labyrinthodonts' from Fort Sill, Oklahoma. On the basis of his findings, PEABODY (1961) discussed palaeoclimatic inferences like alternating wet and dry seasons for this locality.

In 1974, COLDIRON published his work on the possible function of dermal bone sculpture in temnospondyls and other basal tetrapods. He challenged BYSTROW's assumption that the 'rete vasculosum' was functionally associated with cutaneous respiration since the capillaries describe an irregular pathway and thus an inefficient route of the blood to the bone surface and the skin. Based on split-line technique in dermal skull bones of *Alligator* and the orientation of the long-axis orientation in bone cell lacunae of dermal bones of *Eryops*, COLDIRON (1974) inferred the collagen-fiber orientation within the bone. He found the collagen fibers arranged parallel to one another in the internal and middle region, but non-parallel and randomly oriented in the sculptured external region. Thus, COLDIRON (1974) concluded that dermal bone sculpture in basal tetrapods and crocodilians is a strengthening adaptation by distributing the stress that acted on the dermal skull roof.

COSGRIFF & ZAWISKIE (1979) described a capillary network that opens to the sculptured surface in the dermal bones of the rhytidosteid temnospondyl *Pneumatostega*, although they did not prepare thin sections. Following BYSTROW (1947), they interpreted this vascularization as indication of cutaneous respiration.

DE RICQLÈS (1981), in his comprehensive work on long bones of fossil tetrapods, also commented on dermal skull bones of the temnospondyl *Trematops* and the nectridean *Diplocaulus*. In *Trematops* (DE RICQLÈS 1981, pl. 1, fig. 4), he described parallel-fibered bone with simple primary canals in the external cortex, and recognized lamellar-zonal bone in the external cortex of *Diplocaulus* (DE RICQLÈS 1981, pl. 2, fig. 3).

CASTANET et al. (2003) published a useful compilation of the present knowledge on bone histology of extant and extinct amphibians including stem-amniotes and early tetrapods. They confirmed the diploë structure as described by GROSS (1934) and BYSTROW (1935, 1947) as basic pattern for most dermal bones. According to CASTANET et al. (2003), the external cortex consists of primary bone tissue with a lamellar structure and contains simple vascular canals and primary osteons. Zones and annuli (and sometimes lines of arrested growth) indicate that bone deposition was cyclic. The middle spongy or cancellous region has undergone remodeling whose degree varies between

taxa. The internal region is lamellar and usually penetrated by a small number of simple canals that run parallel to the internal bone surface. Sharpey's fibers may cross this region at a steep angle.

In his analysis of placodont osteoderm histology, SCHEYER (2007) also referred to the internal structure of temnospondyl dermal bones and illustrated histological sections of *Trimerorhachis*, *Mastodonsaurus* and *Gerrothorax*. He observed a diploë pattern with a generally high vascularization and secondary remodeling in the middle region. The external and internal cortices consist mainly of parallel-fibered bone with growth marks, and transitions to interwoven structural fibers (ISF) in *Mastodonsaurus* exist. SCHEYER (2007) observed Sharpey's fibers that penetrate the bone of the sculptural ridges in *Mastodonsaurus*.

The aim of the present paper is to close the gap in the literature about dermal bone histology in basal tetrapods, and to provide a basis for comparison with the histology of dermal bones plus the overlying integument in extant sculpture-bearing fishes and tetrapods, that will be carried out in a future paper (WITZMANN in progress). Considered in the present study are dermal bones of the skull and the pectoral girdle, whereas the histology of osteoderms in temnospondyls is dealt with in a separate publication (WITZMANN & SOLER-GIJÓN 2008). Importance is especially attached to the different types of bone tissues, the course of intrinsic bone fibers and the presence of extrinsic fibers. A further focus will be the degree of vascularization and the type and morphology of the vascular canals, and also the mode of growth of the dermal bones, especially of the external sculpture. The results will be taken to draw conclusions about the integument in which these bones were formed, and possible functional aspects of dermal bone sculpture in basal tetrapods will be discussed.

Institutional abbreviations

CMNH	Cleveland Museum of Natural History, Cleveland, Ohio (USA)
MB	Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin, Museum für Naturkunde (Germany)
MCZ	Museum of Comparative Zoology, Harvard, Cambridge/Mass. (USA)
SMNS	Staatliches Museum für Naturkunde Stuttgart (Germany)
UCMP	University of California, Museum of Paleontology, Berkeley (USA)
UMZC	University Museum of Zoology, Cambridge (UK)

Anatomical abbreviations

cl	bone cell lacuna
cr	crevice (artefact)
de	dentine
EC	external cortex
en	enamel
ER	erosion room
fbs	former bone surface
fl	longitudinally cut bone fibers
ft	transversely cut bone fibers
GM	growth marks
IC	internal cortex
IL	interstitial lamellae
ISF	interwoven structural fiber bundles
LB	lamellar bone
MR	middle region
ov	opening of large vessel
PB	primary bone
PFB	parallel-fibered bone
PO	primary osteon
PVC	primary vascular canal
RL	resorption line
ShF	Sharpey's fibers
SB	secondary bone
SO	secondary osteon
tr	trabeculae

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2. Material and methods

Taxa whose dermal bones were investigated histologically by thin sections and their inventory numbers are listed in Table 1. Altogether, 103 histological slides have been prepared from dermal bones of skull and pectoral girdle of 20 taxa of finned and limbed sarcopterygians. The dermal bone fragments were first embedded in synthetic resin (Paraloid B72, an ethyl-methacrylat-copolymere) and then cut vertically either parallel or transverse to the direction of the sculptural ridges. Thin-sections were prepared with a thickness of approximately 30–50 µm using the standard method of CHINSAMY & RAATH (1992). Additionally, one slide of *Plagiosuchus pustuliferus* (FRAAS, 1896) (MB.Hi.1705), one slide of *Plagiosternum granulosum* (FRAAS, 1889) (MB.Hi.1714), and six slides of dermal bones of *Metoposaurus diagnosticus* (VON MEYER, 1842) (MB.Hi.1718–1723) produced by WALTER GROSS in 1934 and stored in the Museum für Naturkunde Berlin,

Tab. 1. Taxa investigated in this study with list of specimens and their inventory numbers.

Taxon	Stratigraphy	Locality	Specimens/Remarks
Porolepiform and stem-tetrapods			
Laccognathus panderi Gross, 1941	Middle Devonian	Riga, Latvia	MB.f.17666: several fragments of dermal skull or pectoral girdle. 4 slides
Panderichthys rhombolepis (Gross, 1930)	Late Devonian, Gauja beds	Latvia	MB.f.17548: several fragments of dermal skull or pectoral girdle. 5 slides
Acanthostega gunnari Jarvik, 1952	Late Devonian, upper Famennian, Britta Dal Formation	Stensiö Bjerg, Greenland	UMZC 150b: 1 fragment of cheek. 3 slides
Greererpeton burkemorani Romer, 1969	upper Viséan/lower Namurian	Greer, West Virginia, USA	CMNH 11900: several fragments of dermal skull. 6 slides
Temnospondyls			
Edops craigi Romer, 1936	Early Permian	Terrapin School, Archer County, Texas, USA	MCZ 1235: 3 fragments of dermal skull roof. 6 slides
Chenoprosopus milleri Mehl, 1913	Early Permian, Cutler Formation	New Mexico, USA	UCMP 41104: 5 pieces of dermal skull roof. 6 slides
Eryops megacephalus Cope, 1877	Early Permian, Moran Formation, Wichita Group	Little Bitter Creek, Young County, Texas, USA	Dermal skull: MCZ 4325: 1 fragment, 7622: 6 fragments; UCMP 203332: 2 fragments. 16 slides
Acheloma cumminsi Cope, 1882	Early Permian, Putnam Formation	Archer County, Texas, USA	MCZ 1490: 3 skull roof fragments. 5 slides
Sclerocephalus haeuseri Goldfuss, 1847	Early Permian, Autunian, Jeckenbach Black Shale Horizon	Heimkirchen, Saar-Nahe Basin, Germany	SMNS 90517: cheek and circumorbital elements of a subadult specimen (c. 120 mm skull length). 1 slide
Archegosaurus decheni Goldfuss, 1847	Lower Permian, Humberg Black Shale Horizon	Lebach, Saar-Nahe Basin, Germany	MB.Am.152: prefrontal, subadult specimen (c. 200 mm skull length). 1 slide
Kupferzellia wildi Schoch, 1997	Middle Triassic, upper Ladinian, upper Lettenkeuper	Kupferzell, Württemberg, Germany	SMNS 91247: fragment of skull table (?supratemporal). 1 slide
Mastodonsaurus giganteus (Jaeger, 1828)	Middle Triassic, upper Ladinian, upper Lettenkeuper	Kupferzell, Württemberg, Germany	Skull roof: SMNS 91248; 91249; 91250; 80878; 91251 91254. 14 slides. Clavicle: SMNS 91255, juvenile. 2 slides
Metoposaurus diagnosticus (von Meyer, 1842)	Late Triassic	Krasiejów, Poland	Dermal bone fragment: MB.Hi.1718 1723; MB.Hi.1721 was figured by Gross (1934: fig. 3). 6 slides produced by Walter Gross
Plagiosuchus pustuliferus (Fraas, 1896)	Middle Triassic, Ladinian, Lettenkeuper	Württemberg, Germany	SMNS 82023: fragment of skull roof. 2 slides; MB.Hi.1705: unidentified dermal bone. 1 slide produced by Walter Gross
Plagiosternum granulosum (Fraas, 1889)	Middle Triassic, Ladinian, Grenzbonebed	Württemberg, Germany	SMNS 91256: interclavicle. 3 slides
Gerrothorax sp.	Middle Triassic, Ladinian, Longobardian	Württemberg, Germany	SMNS 91257, 91258: clavicles; SMNS 91259, 83033: fragments of interclavicle. 8 slides
Lepospondyls			
Diplocaulus magnicornis Cope, 1882	Early Permian, UCMP: Wellington Formation MCZ: Arroyo Formation, Clear Fork Group	UCMP: Orlando, Oklahoma, USA; MCZ: Texas, USA	Fragments of dermal skull roof: UCMP 203658: 5 fragments; 203505: 4 fragments; 203141: 1 fragment; 202966: 1 fragment; MCZ 2269: 4 fragments. 15 slides
Pantylus cordatus Cope, 1881	Early Permian, Wichita Group	Texas, USA	UCMP 20296: fragment of dermal skull roof. 1 slide
Seymouriamorpha			
Seymouria baylorensis Broili, 1904	Early Permian	Baylor County, Clear Fork, West Coffee Creek, Texas, USA	MCZ without number: 1 fragment of the lower jaw (?angular). 3 slides
Eureptilia			
Labidosaurus hamatus Cope, 1895	Early Permian, Clear Fork Group	Texas, USA	MCZ without number: 1 fragment of skull table. 1 slide

were studied. The thin sections were examined by using a Leica DC 300 polarising stereosmicroscope with transmitted ordinary and polarised light. For the investigation of the bone structure by SEM, dermal bone fragments were first cut and polished, and the polished surface was then etched with 10 % HCL for 8 10 seconds.

All dermal bones sectioned in this study are assumed to belong to adults or, in the case of *Sclerocephalus haeuseri* Goldfuss, 1847, *Archegosaurus decheni* Goldfuss, 1847 (based on skull length) and *Acanthostega gunnari* Jarvik, 1952 (based on bone thickness of the cheek), to subadults. The only small juvenile specimen in the sample belongs to *Mastodonsaurus giganteus* (Jaeger, 1828) and is listed and described separately from the adults of this species. For each taxon investigated here, the bone microstructure and histology was consistent. Intraspecific variability was only observed in *Mastodonsaurus giganteus* and *Plagiosternum granulosum* and affects the degree of vascularization of the bone (see description).

The terminology of Francillon-Vieillot et al. (1990) and de Ricqlès et al. (1991) concerning bone histology will be used throughout the text. Furthermore, I follow Scheyer & Anquetin (2008) in their work on turtle shell bone histology in the use of the term 'external' and 'internal'. An appropriate alternative designation is 'superficial' and 'deep', as used by Hill (2006) instead of 'external' and 'internal', respectively. The external sculptured surface of the dermal bone faces the body surface, whereas the internal surface is oriented to the visceral surface of the body. The term 'interior' corresponds to the inner or middle part of the bone. In general, the dermal bones show a diploë structure, i. e., a middle region that is cancellous or trabecular is mantled by compact external and internal cortices. Three-dimensionally interwoven bundles of collagen fibers with a well ordered fiber bundle arrangement showing no general isotropy under polarized light are designated here as 'interwoven structural fibers' (ISF) (Scheyer & Sander 2004; Scheyer & Sánchez-Villagra 2007; Scheyer 2007; Scheyer & Anquetin 2008). They are distinguished from woven or fibrous bone that shows general isotropy and the collagen fibers of which are irregularly and loosely arranged (Francillon-Vieillot et al. 1990; de Ricqlès et al.

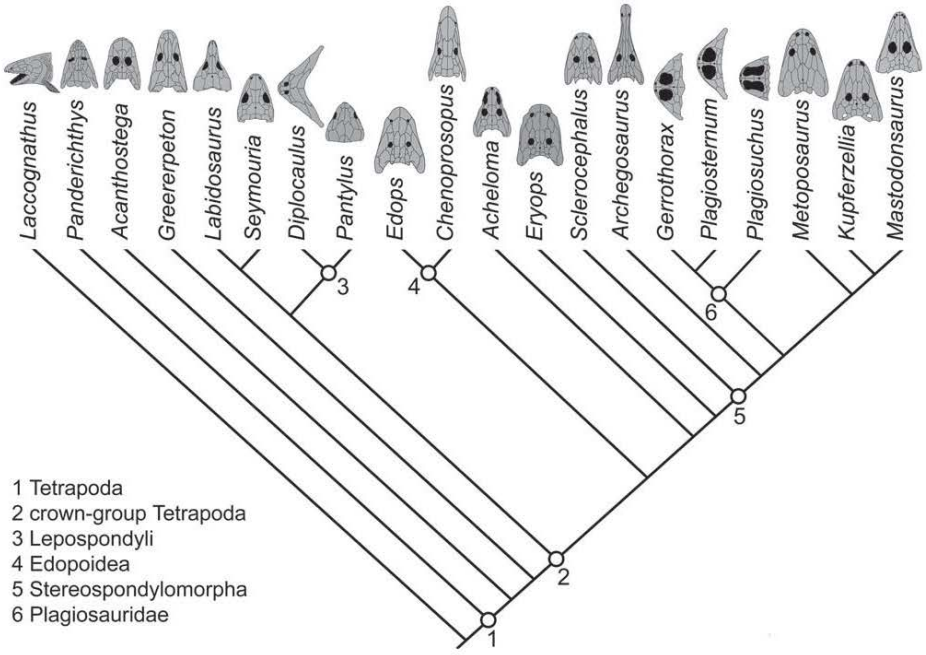

Fig. 1. Phylogenetic relationship of the taxa investigated in this study. After Yates & Warren (2000), Ruta et al. (2003) and Schoch & Witzmann (2009).

1991). The sculptural tubercles and ridges on the external surface of the dermal bones are called 'saddles' and the grooves between them as 'valleys' in the thin sections. Canaliculi that are longer than the maximum diameter of the appertaining bone cell lacuna are designated as 'long', those that are approximately as long as the maximum diameter are 'moderately long', and those whose length is shorter than maximum diameter are termed 'short'.

The interrelationships of basal tetrapods as found in the analyses of YATES & WARREN (2000), RUTA et al. (2003) and SCHOCH & WITZMANN (2009) are taken as the phylogenetic framework of this study (Fig. 1). The term 'crown-group tetrapod' is used here in the sense of HENNIG (1966) as encompassing the last common ancestor of all living tetrapods and all its descendants, fossil and extant. The stem-group tetrapods define all fossil taxa that are more closely related to crown-group tetrapods than to the extant group that is most closely related to crown-group tetrapods (either actinistians [e. g., ZHU & SCHULTZE 2001] or dipnoans [e. g., CLOUTIER & AHLBERG 1996]).

3. Description of histological thin sections

3.1. Outgroup finned sarcopterygian

3.1.1. *Laccognathus panderi* (Porolepiformes)

The external surface of the dermal skull bones of *Laccognathus panderi* GROSS, 1941 bears a sculpture of small, round to oval tubercles that give the bone a pustular appearance. The sectioned bone has a thickness of approximately 4.5 mm, and the ratio external cortex : middle region : internal cortex is 1 : 1.5 : 0.6.

E x t e r n a l c o r t e x . As described by PANDER (1860), GROSS (1930) and ØRVIG (1957), the tubercles of the external bone surface represent odontodes ('dermal teeth') consisting of dentine with a cap of enamel (Fig. 2a–c), and several odontodes of earlier generations can be found 'buried' within the bone matrix of the external cortex and may be in the state of resorption. In some regions, the external bone surface of an earlier growth phase can readily be traced as a sharp red-brownish line, extending from odontode to odontode. Sometimes this line is scalloped out to receive a vascular canal (Fig. 2a). Short, fine Sharpey's fibers that measure approximately 2 µm in diameter cross the former external bone surface at approximately a right angle (Fig. 2a). They are regularly but not densely arranged, are hollow inside and filled by organic substance, indicating that they were not or only poorly mineralized in the living animal. The external cortex is composed mainly of fine parallel-fibered bone (Fig. 2b). Its fibers show regional changes in orientation: fibers that course approximately parallel to the surface of the section appear bright or dark under polarized light, depending on the orientation of the slide, and have spindle-shaped bone cell lacunae that are bipolar, i. e., they possess short canaliculi at both tapering ends. Fibers that are cut approximately perpendicularly remain dark under polarized light and the bone cell lacunae appear round. Vascularization is high and consists of anastomosing primary vascular canals and primary osteons, that are often aligned in layers.

M i d d l e r e g i o n . The external cortex grades into the coarse cancellous and well vascularized middle region that possesses several primary and secondary osteons (Fig. 2c). In some areas, the bone is trabecular with large, irregularly shaped erosion rooms. The trabeculae are irregular in outline and lack lining of secondary bone. The primary bone matrix consists of parallel-fibered bone whose fibers show regionally different orientations, similar to the external region. Near the transition to the internal cortex, the bone matrix of the middle region contains several primary osteons aligned in rows.

I n t e r n a l c o r t e x . The internal cortex is separated from the middle region by a distinct transition. As outlined by PANDER (1860) and GROSS (1930), the internal cortex of *Laccognathus* exhibits a plywood-structure that can be designated as isopedine (Fig. 2d). In polarized light, a regular pattern of horizontal bands is visible. Those bands in which the fibers are cut longitudinally appear bright or dark under polarized light (with elongate cell lacunae), depending on the orientation of the slide, whereas those in which the fibers and bone cell lacunae are obliquely cut brighten up to a lesser extent. Bands with transversely cut fibers remain dark in polarized light (with round cell-lacunae) and exhibit a fine bright meshwork that delineates the single fiber bundles. Fine fibers, which are oriented approximately perpendicular to the internal bone surface, are discernable also in normal transmitted light. The internal cortex is avascular.

3.2. Stem-group tetrapods

3.2.1. *Panderichthys rhombolepis* ("Elpistostegalia")

The dermal skull bones of *Panderichthys rhombolepis* (GROSS, 1930) bear basically a tubercular sculpture, and low sculptural ridges may connect the tubercles. The thickness of the sectioned bones amounts approximately 4 mm. The ratio external cortex : middle region : internal cortex is 1 : 0.8 : 0.4.

E x t e r n a l c o r t e x . The dermal bones of *Panderichthys* lack any dentine and enamel components, so that the sculptural tubercles and ridges are composed solely of bone tissue (Fig. 2e). Similar to odontodes, 'buried' tubercles of earlier generations are visible in the external region. As in *Laccognathus,* the bone matrix consists of

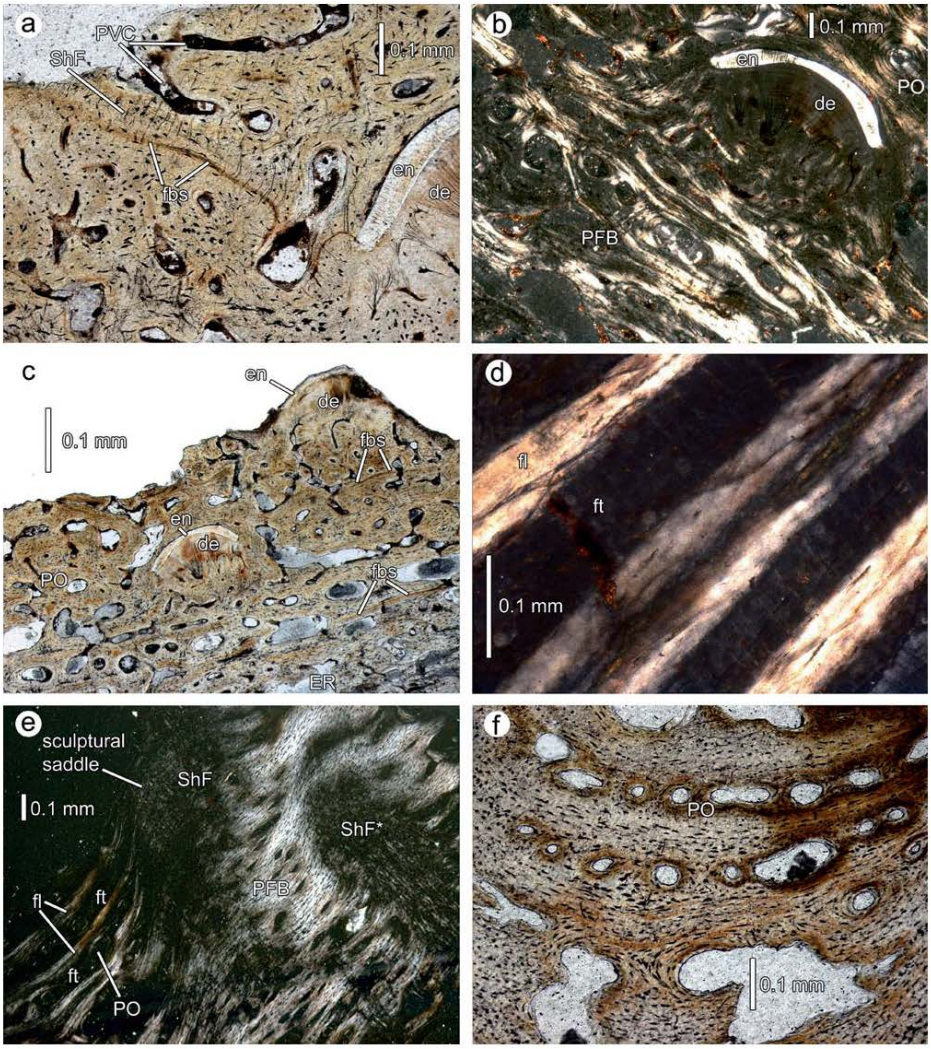

Fig. 2. **a**–**d**. *Laccognathus panderi* Gross, 1941, MB.f.17666. Vertical sections of dermal bones of skull or pectoral girdle. **a**. External cortex in normal transmitted light; next to the odontode, the bone surface of an earlier growth stage with perpendicular, unmineralized Sharpey's fibers is visible. **b**. External cortex with odontode in polarized light. **c**. External cortex with two odontodes and external part of middle region in normal transmitted light; primary and secondary osteons are arranged in rows. **d**. Internal cortex consisting of isopedine, polarized light. – **e**–**f**. *Panderichthys rhombolepis* (Gross, 1930), MB.f.17548. Vertical sections of dermal bones of skull or pectoral girdle. **e**. External cortex in polarized light with sculptural valley and saddle, which consists solely of bone, the asterisk (*) indicates a 'buried' sculptural saddle of an earlier generation. **f**. Rows of primary osteons in a sculptural valley, normal transmitted light. – For abbreviations, see text.

fine parallel-fibered bone whose fibers show locally different orientations. Growth marks cannot be detected. Vascularization is moderate and consists of a succession of layers of primary osteons interior to the sculptural valleys, and more interiorly, larger erosion cavities are visible (Fig. 2f). These layers of primary osteons are located in a parallel-fibered bone matrix with mostly transversely cut fibers (remain dark under polarized light) and round cell lacunae (Fig. 2e, f). Between these layers, layers of parallel-fibered bone whose fibers are cut longitudinally with spindular, bipolar bone cell lacunae are intercalated. This gives the bone the appearance of alternating dark and bright bands that wedge out at the lateral bases of the sculptural saddles under polarized light (Fig. 2e, on the left). In contrast to the valleys, the saddles are poorly vascularized by primary vascular canals, whereas more interiorly, several anastomosing primary vascular canals are present. Fine Sharpey's fibers that extend far interiorly until to the middle region penetrate the sculptural saddles, both in the superficial saddles and in the 'buried' ones of earlier generations, but are absent in the valleys (Fig. 2e). The Sharpey's fibers have a diameter of 5 to 6 µm. In polarized light, the Sharpey's fibers appear bright and dark, respectively, depending on the orientation of the slide. This indicates that they were well mineralized in the living animal.

Middle region. This region is coarse cancellous. In the more interior part, the region is trabecular with irregular, thin to moderately thick trabeculae that enclose large erosion cavities that are lined by secondary bone lamellae (Fig. 3a). The primary matrix consists mostly of fine parallel-fibered bone. Several smaller secondary osteons are present and some of them cut each other, but do not form Haversian tissue. The middle region is separated from the internal cortex by a distinct transition.

Internal cortex. The internal cortex consists of isopedine, similar to the internal cortex of *Laccognathus*, but appears less regular, since the bands are of different thickness and may fray out at their lateral ends (Fig. 3b). Fine fibers that are approximately perpendicular to the internal bone surface are visible in the dark bands. Scattered primary vascular canals run parallel or oblique to the internal bone surface.

3.2.2. *Acanthostega gunnari*

The investigated sections of *Acanthostega gunnari* JARVIK, 1952 were prepared through the cheek region (probably the squamosal, whose bone thickness varies between 1 mm and 3 mm) with polygonal sculpture. The ratio external cortex : middle region : internal cortex is 1 : 1.8 : 0.9.

External cortex. The bone matrix consists of parallel-fibered bone that is mostly homogeneous, whereas in some regions, it appears coarse and less regular (Fig. 3c, d). As in the finned sarcopterygians desribed above, the bone fibers may change their orientation in different regions, and this is reflected by the shape of the bone cell lacunae. The bone is moderately to highly vascularized by primary vascular canals and primary osteons. Loosely arranged Sharpey's fibers with a diameter of 3 to 5 µm penetrate the sculptural saddles until to the middle region (Fig. 3c), but they can also be found in the valleys where they are less abundant. Growth marks are not visible in the external cortex.

Middle region. This region is coarse cancellous with primary osteons and several, partially large secondary osteons (Fig. 3d). The bone matrix consists of fine parallel-fibered bone and of the lamellar bone of the secondary osteons.

Internal cortex. Isolated primary vascular canals may locally be present and run parallel to the internal bone surface. The bone matrix is composed of parallel-fibered bone that appears fine in most regions, but may also change its fiber orientation in irregular layers, so that the internal cortex resembles irregular isopedine in some regions (Fig. 3e). Fine fibers are visible that cross the internal cortex approximately at a right angle.

3.2.3. *Greererpeton burkemorani* (Colosteidae)

Greererpeton burkemorani ROMER, 1969 has strongly sculptured dermal bones with high sculptural ridges. The skull fragment used for sectioning (?quadratojugal) has a sculpture of polygons and furrows of irregular outline, and its thickness ranges from 3.5 mm to more than 5 mm. The ratio external cortex : middle region : internal cortex is 1 : 1.4 : 1.3.

External cortex. As in the taxa described above, the bone matrix of the external cortex consists mainly of parallel-fibered bone the fibers of which show varying orientation in some regions (Fig. 3f), what is reflected in the shape of the bone cell lacunae (Fig. 4a). The intrinsic fibers of the parallel-fibered bone are mostly coarse and vary in extent and direction what gives the bone tissue often a less ordered appearance. Fine Sharpey's fibers (Fig. 3f) that are well mineralized penetrate the external region at approximately a right angle to the surface and are more abundant in the sculptural saddles than in the valleys. The Sharpey's fibers have a diameter of 3 to 7 µm. The external region is well vascularized by partially anastomosing primary vascular canals (Fig. 4a) and scattered primary osteons. Growth marks cannot be observed.

Middle region. The external cortex grades into a fine to coarse cancellous region that is very well vascularized by numerous primary and secondary osteons whose

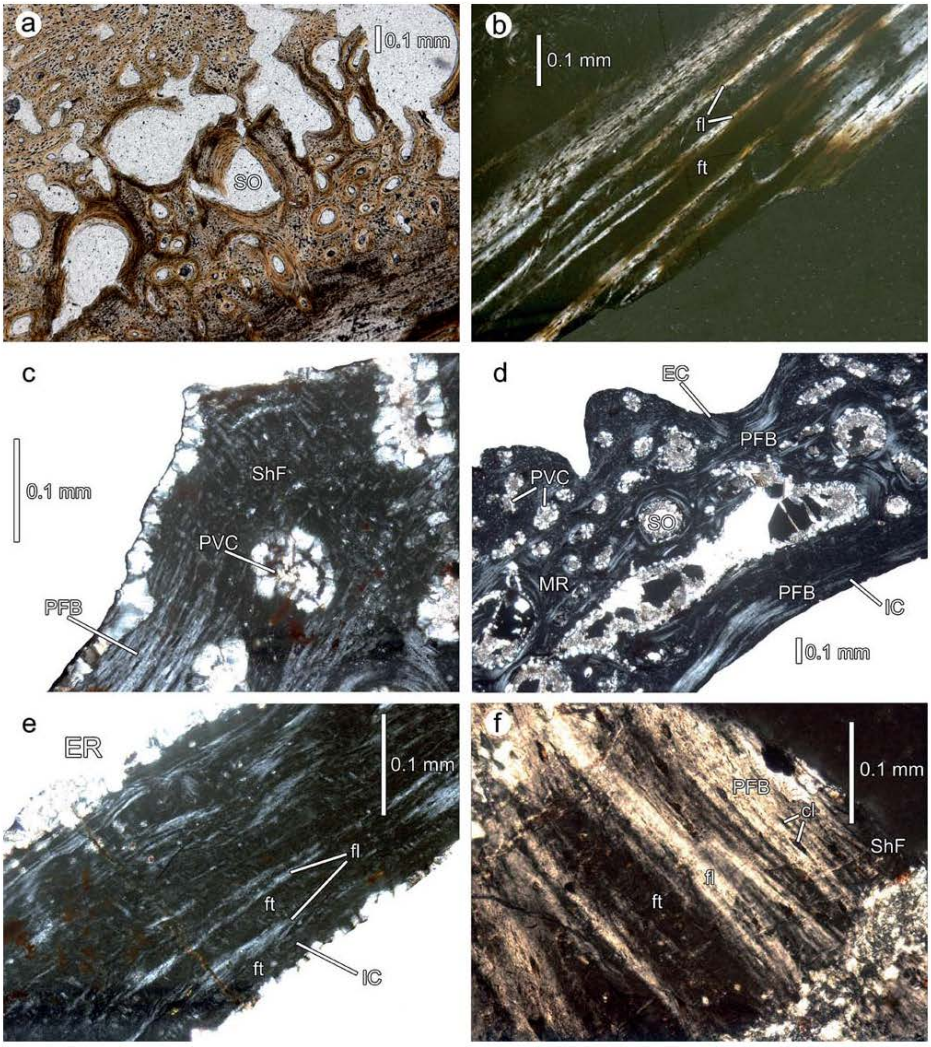

Fig. 3. a–b. *Panderichthys rhombolepis* (Gross, 1930), MB.f.17548. Vertical sections of dermal bones of skull or pectoral girdle. **a.** Middle region in normal transmitted light with secondary osteons. **b.** Internal cortex consisting of isopedine, polarized light. – **c–e.** *Acanthostega gunnari* Jarvik, 1952, UMZC T 150b. Vertical section of the cheek, probably squamosal. **c.** Sculptural saddle of external cortex with Sharpey's fibers and primary vascular canals, polarized light. **d.** Histological overview in polarized light, the external cortex is well vascularized, and secondary remodeling took place in the middle region. **e.** Internal region in polarized light, the bone fibers may show changing orientation in different layers, so that it has locally an isopedine-like appearance. – **f.** *Greererpeton burkemorani* Romer, 1969, CMNH 11900. Vertical sections of dermal skull bone (?quadratojugal). Low sculptural saddle of external cortex in polarized light; the parallel-fibered bone shows regional changes of its bone fiber orientation, and thin Sharpey's fibers are present. – For abbreviations, see text.

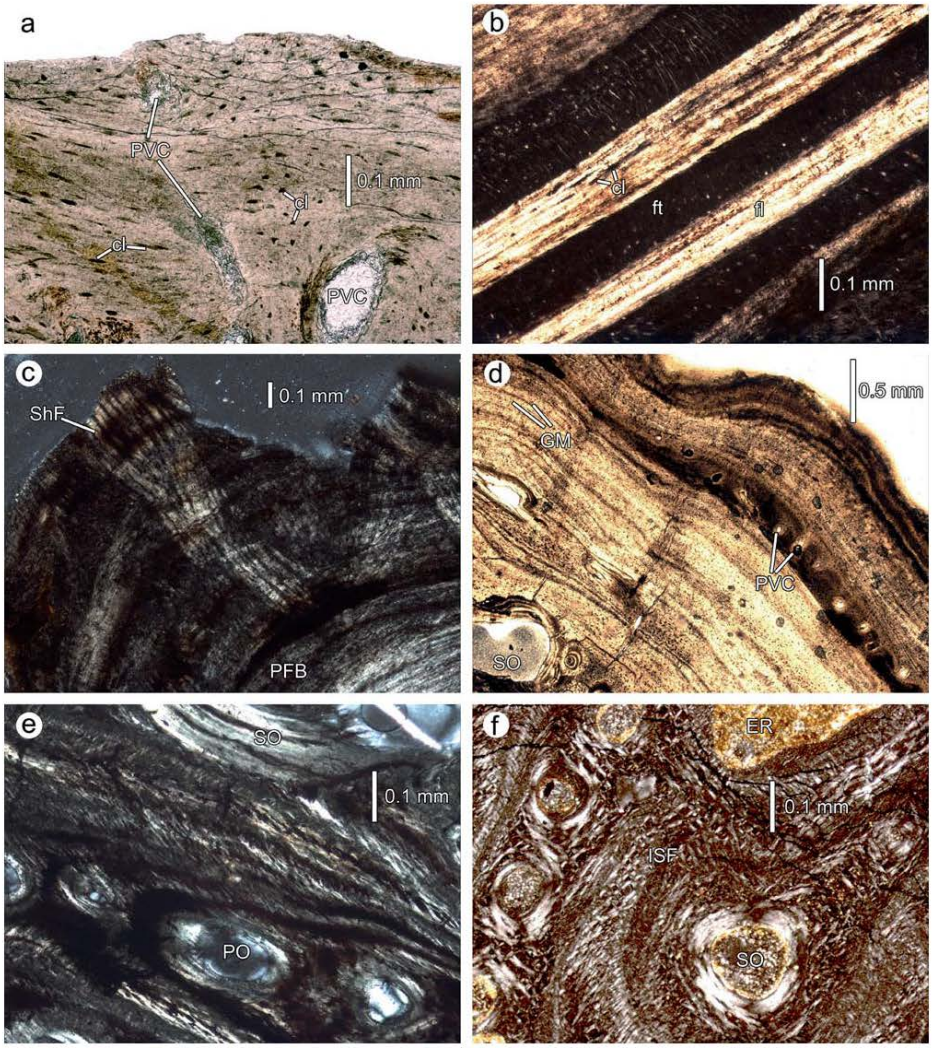

Fig. 4. a–b. *Greererpeton burkemorani* ROMER, 1969, CMNH 11900. Vertical sections of dermal skull bone (?quadratojugal). **a.** Low sculptural saddle of external cortex in normal transmitted light, the shape of the bone cell lacunae represents the direction of the bone fibers: on the left, the lacunae are spindular and indicate that the fibers are oriented parallel to the image plane, and on the right, the lacunae are round and indicate transverse section of the fibers. **b.** Internal cortex consisting of isopedine in polarized light. – **c–f.** *Edops craigi* ROMER, 1936, MCZ 1235. Vertical section of skull table bone. **c.** External cortex, sculptural saddle with Sharpey's fibers, polarized light. **d.** External cortex showing growth marks and sparse vascularization, normal transmitted light. **e.** Middle region with primary matrix of fine, subparallel fibers and primary and secondary osteons, polarized light. **f.** Middle region with interwoven structural fibers as primary tissue, polarized light. – For abbreviations, see text.

Haversian canals may constitute large cavities, but true Haversian tissue cannot be observed. The interstitial, primary bone matrix consists of fine parallel-fibered bone.

Internal cortex. The compact internal cortex consists of isopedine, and the shape of the bone cell lacunae reflects the orientation of the fibers. However, the discrete bands exhibit a broad variation in their thickness (Fig. 4b). Most parts of the internal cortex are avascular, but in the most interior part, isolated primary vascular canals and few secondary osteons are visible that are parallel to the internal bone surface. Fine fibers that are arranged perpendicular to the internal bone surface are visible in the 'dark layers'.

3.3. Crown-group tetrapods

3.3.1. *Edops craigi* (Temnospondyli, Edopoidea)

The bone fragments of *Edops craigi* Romer, 1936 used for sectioning stem from the skull table and bear a rather irregular, polygonal sculpture of ridges and pits. Histologically, the middle region of the bone is much thickened with respect to the cortices. The sectioned bone fragments attain a thickness of more than 12 mm. The ratio external cortex : middle region : internal cortex is 1 : 3.6 : 0.6.

External cortex. In large areas, the external cortex consists of coarse parallel-fibered bone with spindular bone cell lacunae that have long, branching canaliculi. Distinct growth marks are present, and the bone can thus be designated as lamellar-zonal (Fig. 4c, d). Vascularization is in most parts low and consists of isolated primary vascular canals and few primary osteons that may be aligned in single rows (Fig. 4d). Sculptural saddles of earlier generations are embedded within the cortex. Fan-shaped clusters of densely arranged Sharpey's fibers appear irregularly in the sculptural saddles, where they penetrate the bone tissue (Fig. 4c). In the sculptural valleys, the fibers are less numerous. The sometimes bifurcating Sharpey's fibers measure around 21 µm in diameter and may extend to the middle region. In some areas more interior within the cortex, primary interwoven structural fiber bundles (ISF) sensu Scheyer & Sánchez-Villagra (2007) are present and show a non-homogeneous distribution. Such interwoven structural fibers are more abundant in the middle region and are therefore described below. The outer parts of the external layer are in few places disturbed by areas of secondary bone remodeling with a distinct resorption line. These resorption structures at the bone surface are described in more detail for *Eryops* (see below). The external cortex is separated from the middle region by a distinct transition, with the occurrence of several small secondary osteons.

Middle region. This fine to coarse cancellous region underwent extensive remodeling with numerous secondary osteons that constitute Haversian tissue in many areas. The interstitial primary bone consists in many areas of parallel-fibered bone. Rather fine primary fibers that are oriented subparallel, but may change their direction in succeeding layers, can frequently be observed (Fig. 4e). These layers can be arranged irregularly in a 'flowmark'-like fashion. In some areas or layers, primary fibers cross each other at an angle of approximately 90° and constitute a three-dimensional network of interwoven structural fibers (Fig. 4f). Under polarized light, the birefringence patterns of the collagen fibers are well visible. Approximately transversely cut fiber bundles have a globular appearance. Focusing on different planes of the slide under the microscope shows that these structures do not represent real globules like cell spaces, for instance, but fibers that extend perpendicularly or obliquely to the image plane. Between the fibers, bone cell lacunae of irregular outline with no or only stumpy canaliculi are present. These areas of fibers are remains of primary bone, which was remodelled and partially bounded by secondary bone. Near the internal cortex, primary osteons may be aligned regularly in layers.

Internal cortex. Only parts of the compact internal cortex are preserved. As far as it can be discerned, it consists of coarse, less organized parallel-fibered bone that is avascular.

3.3.2. *Chenoprosopus milleri* (Temnospondyli, Edopoidea)

Bone fragments of the skull table of *Chenoprosopus milleri* Mehl, 1913 were sectioned that bear a sculpture of rounded polygons. The internal part of the middle region, and the complete internal cortex are eroded. The thickness of the sectioned bone fragments ranges from 3 mm to 6 mm.

External cortex. The external cortex is mainly composed of coarse parallel-fibered bone that shows cyclic growth marks (lamellar-zonal bone). The bone cells are variable in outline with varying length of their canaliculi, and are randomly distributed. In the external part of the sculptural saddles, densely arranged Sharpey's fibers with a diameter of 8 to 17 µm are present (Fig. 5a). Some of the fibers may extend until to the external part of the middle region. The fibers may ramify into two or three branches. In the sculptural valleys, the Sharpey's fibers are less numerous than in the saddles and may also be absent in places. In the more interior part of the external cortex, the parallel-fibered bone shows transitions to a network of interwoven structural fibers that extend obliquely to the bone surface (Fig. 5b). The bone cell lacunae in this bone tissue are irregularly arranged and pos-

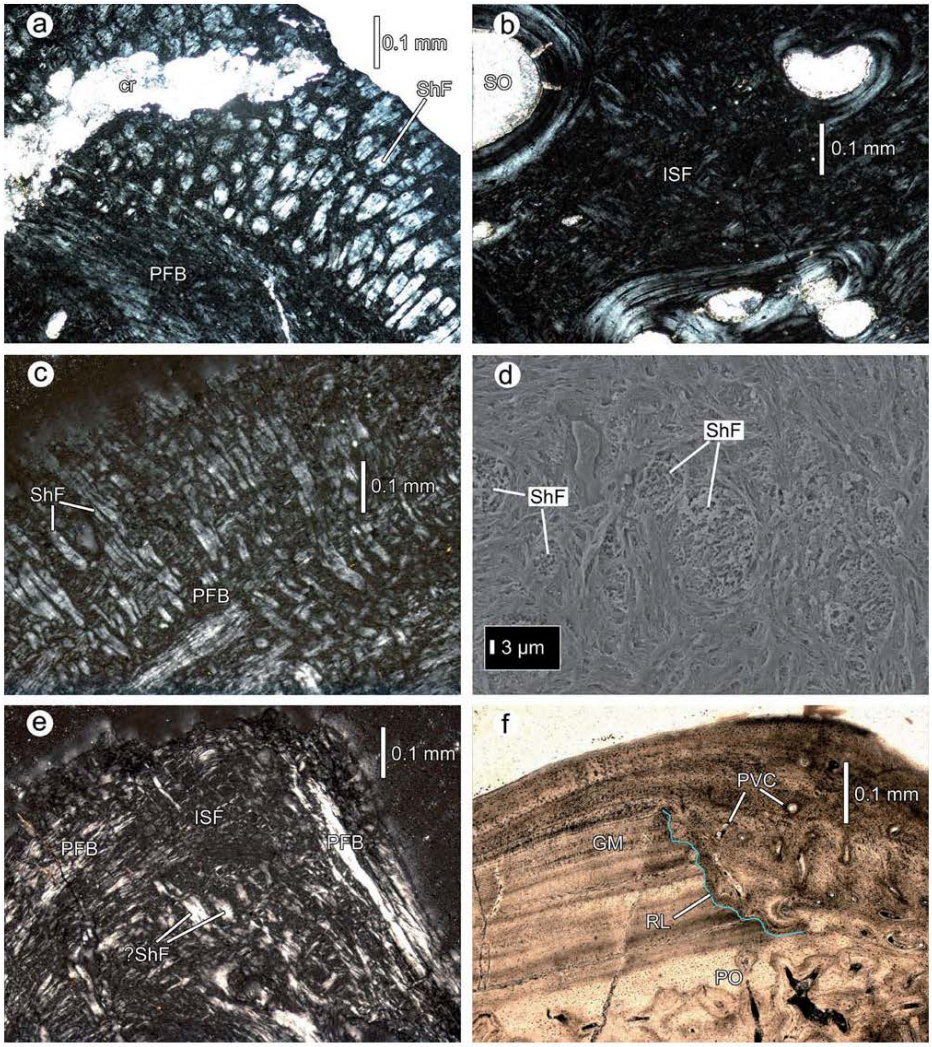

Fig. 5. a–b. *Chenoprosopus milleri* MEHL, 1913, UCMP 41104. Vertical section of skull table bone. **a.** Sculptural saddle of external cortex consisting of parallel-fibered bone with strong bundles of Sharpey's fibers that are obliquely cut, polarized light. **b.** More interior part of external cortex with interwoven structural fibers, polarized light. – **c–f.** *Eryops megacephalus* COPE, 1877. Vertical section of dermal skull bones. **c.** MCZ 7622, external cortex with parallel-fibered bone and bundles of Sharpey's fibers, polarized light. **d.** UCMP 203332, SEM of horizontally cut external cortex with Sharpey's fibers in cross-section. **e.** MCZ 7622, sculptural saddle in polarized light showing parallel-fibered bone and interwoven structural fibers. **f.** MCZ 7622, vertical section of external cortex with secondary remodeling in the externalmost part; the boundary between primary bone and remodelled bone is indicated as a blue line. – For abbreviations, see text.

sess no canaliculi. The external cortex is poorly vascularized with scattered primary vascular canals and isolated primary osteons. In one slide, a layer of primary osteons is visible interior to a sculptural valley. The external cortex grades into the middle region with the occurrence of scattered secondary osteons that increase in number and density in a small transitional zone.

Middle region. This fine to coarse cancellous region is characterized by extensive remodeling of the bone. Numerous secondary osteons that may course in different directions are present that in parts build Haversian tissue. The interstitial primary bone consists of parallel-fibered bone that shows transitions to fine interwoven structural fibers in some regions.

3.3.3. *Eryops megacephalus* (Temnospondyli, Eryopidae)

The bone fragments of the dermal skull roof of *Eryops megacephalus* Cope, 1877 sectioned for this study bear pits of variable outline, and thus the sculpture appears rather irregular. The ratio external cortex : middle region : internal cortex is 1 : 3.3 : 0.6. The bone fragments used for sectioning attain a thickness of more than 14 mm.

External cortex. Densely arranged Sharpey's fibers with a diameter of mostly 21 to 29 µm penetrate the external cortex until to the middle region (Fig. 5c, d). The Sharpey's fibers may be numerous also in the valleys. Coarse, often less ordered parallel-fibered bone predominates the bone matrix of the external cortex and has bone cell lacunae of variable shape that are arranged in rows and have branching, moderately long to long canaliculi. The bone matrix shows local islets of interwoven structural fibers especially in the more interior parts of the cortex, but they may also be present individually in the more external parts (Fig. 5e). Conspicuous growth marks are present in the external cortex (Fig. 5f). Similar to *Edops*, the more superficial parts of the external cortex may be disturbed by areas of secondary bone remodeling (Fig. 5f). The remodelled bone lies discordantly on the primary bone, separated by a distinct resorption line. Whereas the adjacent primary bone is only sporadically pervaded by primary vascular canals and primary osteons, the secondary bone is well vascularized. It consists of parallel-fibered bone and interwoven structural fibers and lacks the clear zonal pattern. In specimen MCZ 7622-2, the remodelled area was subsequently overgrown by 'normal' parallel-fibered bone.

Middle region. The external cortex is separated from the middle region by a short transition zone that contains scattered secondary osteons. The middle region is mostly fine to coarse cancellous and shows extensive remodeling with Haversian tissue (Fig. 6a, b). Also subordinate areas are present in which large vascular spaces are separated by irregularly arranged trabeculae that are rather thick and short. The interstitial primary bone consists of parallel-fibered bone and of the three-dimensional network of interwoven structural fibers (Fig. 6b–d), as described for *Edops*. The transversely cut fibers are visible as 'globules', and between the fibers, bone cell lacunae of irregular outline with no or short canaliculi are visible (Fig. 6c).

Internal cortex. This only fragmentarily preserved region consists mostly of coarse parallel-fibered bone with a less ordered appearance. Transitions to islets of interwoven structural fibers may occur in some areas. Fine, oblique extrinsic fibers that are densely arranged and probably represent Sharpey's fibers cross the internal cortex in MCZ 7622-2. The cortex is poorly vascularized by scattered primary osteons and primary vascular canals.

3.3.4. *Acheloma cumminsi* (Temnospondyli, Dissorophoidea, Trematopidae)

The bone fragments of the dermal skull roof of *Acheloma cumminsi* Cope, 1882 used for sectioning possess rather regular, rounded sculptural pits on their external surface. The bone fragment investigated has a thickness of almost 9 mm, and the ratio external cortex : middle region : internal cortex is 1 : 6.1 : 1.2.

External cortex. The bone matrix is constituted by mostly homogeneous, fine parallel-fibered bone. Vascularization is poorly developed and consists of few primary vascular canals and primary osteons. The sometimes bifurcating Sharpey's fibers with a diameter of 15 to 31 µm are conspicuous. They are restricted to the sculptural saddles where they are moderately to densely arranged (Fig. 6e). Growth marks are present, but are indistinct and difficult to follow. Bone cell lacunae are often oval in shape and possess branching canaliculi. They are more orderly arranged in the valleys than in the saddles, where they have frequently a rather round shape.

Middle region. The transition from the external and internal cortex to the trabecular middle region is abrupt. The middle region underwent strong resorption and remodeling and possesses numerous bone cavities of irregular shape and size, most of which are lined by secondary lamellar bone. The rather short trabeculae are irregularly arranged. The primary bone matrix in the trabeculae consists of homogeneous parallel-fibered bone.

Internal cortex. This region is made of avascular, fine parallel-fibered bone, which is penetrated in some areas by thin fibers at an angle of approximately 60°. Bone cell lacunae are spindular, have long, branching canaliculi and are arranged in rows (Fig. 6f). They may form dark layers of densely arranged lacunae within the internal cortex.

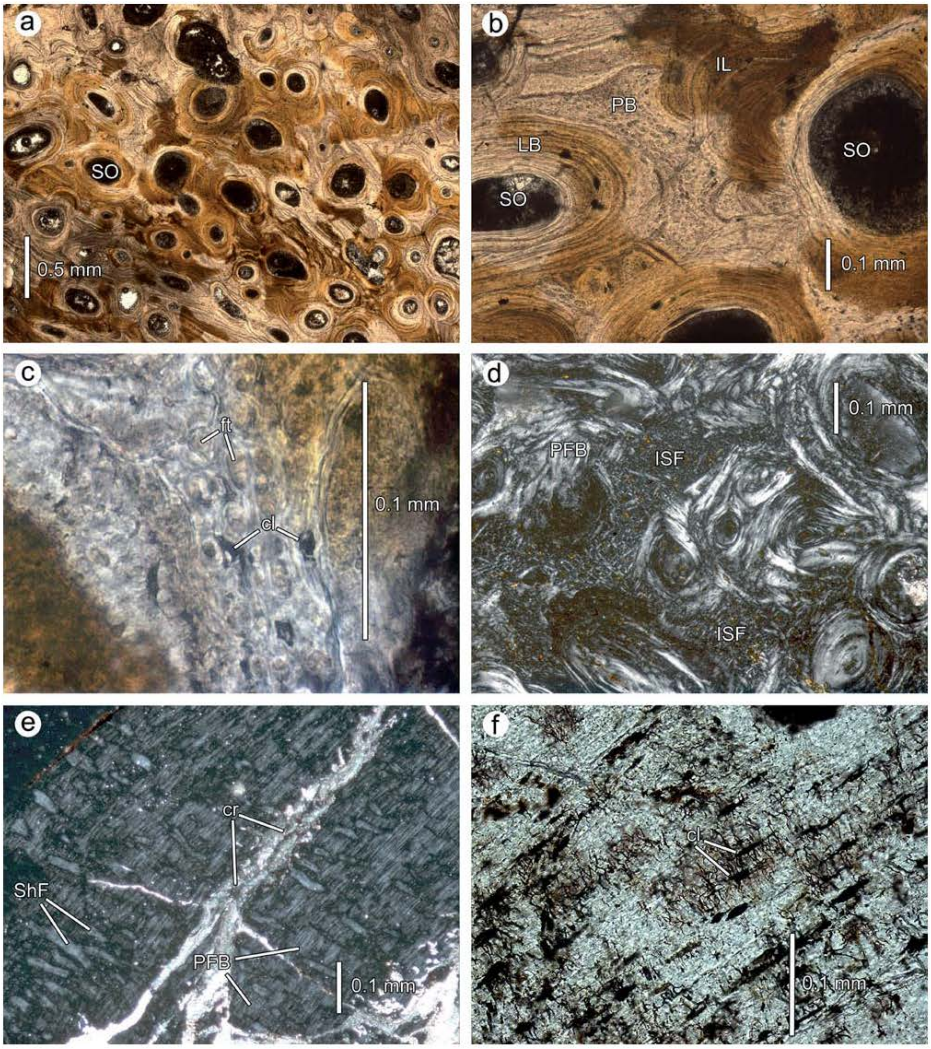

Fig. 6. **a**–**d**. *Eryops megacephalus* Cope, 1877, MCZ 7622. Vertical sections of dermal skull bones. **a**. Overview of middle region with Haversian tissue, normal transmitted light. **b**. Middle region with secondary osteons and interstitial primary bone tissue, normal transmitted light. **c**. Close up of interstitial primary bone tissue of middle region, showing 'globular' fibers in cross section, normal transmitted light. **d**. Middle region in polarized light, showing primary interwoven structural fibers. – **e**–**f**. *Acheloma cumminsi* Cope, 1882, MCZ 1490. Vertical section of skull roof fragment. **e**. Sculptural saddle of parallel-fibered bone with Sharpey's fibers in polarized light. **f**. Internal cortex with bone cell lacunae, normal transmitted light. – For abbreviations, see text.

3.3.5. *Sclerocephalus haeuseri* (Temnospondyli, Stereospondylomorpha)

The postfrontal of a subadult specimen of *Sclerocephalus haeuseri* GOLDFUSS, 1847 was sectioned. The bone has a maximum thickness of 4.2 mm, and the ratio external cortex : middle region : internal cortex amounts 1 : 4.2 : 1.1. Unfortunately, the bone was heavily altered by recrystallization, so that nothing can be said about the bone tissue itself or the intrinsic and extrinsic fibers. However, the slide shows the vascularization of the cortices, the bone's microstructure and growth marks. The bone structure is best visible in reflected light (Fig. 7a, b). The external cortex is moderately to low vascularized by primary vascular canals (Fig. 7a). Bone cell lacunae are abundant, but their exact shape cannot be determined. Cyclical growth marks are conspicuous and follow the relief of the external bone sculpture. The middle region can be designated as trabecular with large erosion rooms that are lined by secondary lamellar bone (Fig. 7a, b). The internal cortex is poorly vascularized by scattered primary vascular canals.

3.3.6. *Archegosaurus decheni* (Temnospondyli, Stereospondylomorpha)

A prefrontal of a subadult specimen of *Archegosaurus decheni* GOLDFUSS, 1847 was sectioned. The external bone surface possesses a polygonal sculpture in the ossification centre and radiating ridges in the periphery. Unfortunately, the external portion of the external cortex is eroded. This is rather common in *Archegosaurus*, since the specimens are preserved in siderite concretions (geodes) and divide into part and counterpart when the concretions are split. Because of this surface erosion, the ratio between the thickness of the cortices and the middle region cannot be calculated. The maximum thickness of the bone is approximately 2.5 mm.

External cortex. The preserved parts of the external cortex consist homogenously of parallel-fibered bone that is moderately to highly vascularized by primary canals, primary osteons (partially anastomosing) and, more interiorly, by secondary osteons (Fig. 7c). The latter mark the transition zone to the middle region. Bone cell lacunae are numerous, randomly arranged in the primary bone matrix and are of varying shape. The canaliculi are moderately long to long and branching. Sharpey's fibers that penetrate the external bone surface are not visible (probably due to erosion of the external portion of the cortex). However, the prefrontal forms a rather thin, underplating shelf for articulation with the lacrimal; in this region, densely arranged, almost horizontally oriented Sharpey's fibers are visible that connected the two adjacent bones (Fig. 7d).

Middle region. The trabecular middle region experienced extensive erosion and remodeling. Large erosion rooms, some of them lined by secondary lamellar bone, are separated from each other by trabeculae of irregular outline and direction (Fig. 7c). Many of the trabeculae are stout, others are slender and long. The interstitial bone matrix of the trabeculae may contain small primary or secondary osteons, which are sometimes cut. The primary matrix of the middle region consists of parallel-fibered bone, and morphology and alignment of the bone cells corresponds to those of the external cortex.

Internal cortex. The internal cortex is separated from the trabecular middle region by a thin transition zone with small secondary osteons (Fig. 7c) and consists of rather coarse parallel-fibered bone. The matrix is penetrated by scattered primary vascular canals that course in different directions. Bone cell lacunae are aligned in rows and have an elongate, flattened shape with long, branching canaliculi.

3.3.7. *Kupferzellia wildi* (Temnospondyli, Stereospondylomorpha, Capitosauroidea)

The bone fragment of *Kupferzellia wildi* SCHOCH, 1997 under study is derived from the skull table and probably represents a part of the supratemporal. Its dermal sculpture consists of rather regular, wide polygons. The thickness of the investigated bone amounts slightly more than 5 mm, and the ratio external cortex : middle region : internal cortex is 1 : 1.7 : 0.5.

External cortex. The bone matrix consists mainly of coarse parallel-fibered bone with a rather irregular fibrous arrangement (Fig. 7e). In the sculptural saddles, the parallel-fibered bone is even less organized than in the valleys. The external cortex is moderately vascularized: more externally, only isolated, small primary vascular canals and primary osteons are visible, whereas more interiorly, a larger number of small primary canals and primary osteons (as well as few secondary osteons) are present and may anastomose. Sharpey's fibers are restricted to the sculptural saddles and measure 5 to 16 µm in diameter. In the parallel-fibered bone of the sculptural valleys, the bone cell lacunae are mostly spindular with long canaliculi and are arranged in layers. In contrast, their shape is variable in the more coarse parallel-fibered bone of the saddles. Growth marks are present but difficult to follow.

Middle region. This region is coarse cancellous with several secondary osteons of varying size, but Haversian tissue is not present (Fig. 7f). In the interior part, the Haversian canals may be quite large. The primary matrix consists of fine parallel-fibered bone with generally spindular cell lacunae. Local transitions to interwoven struc-

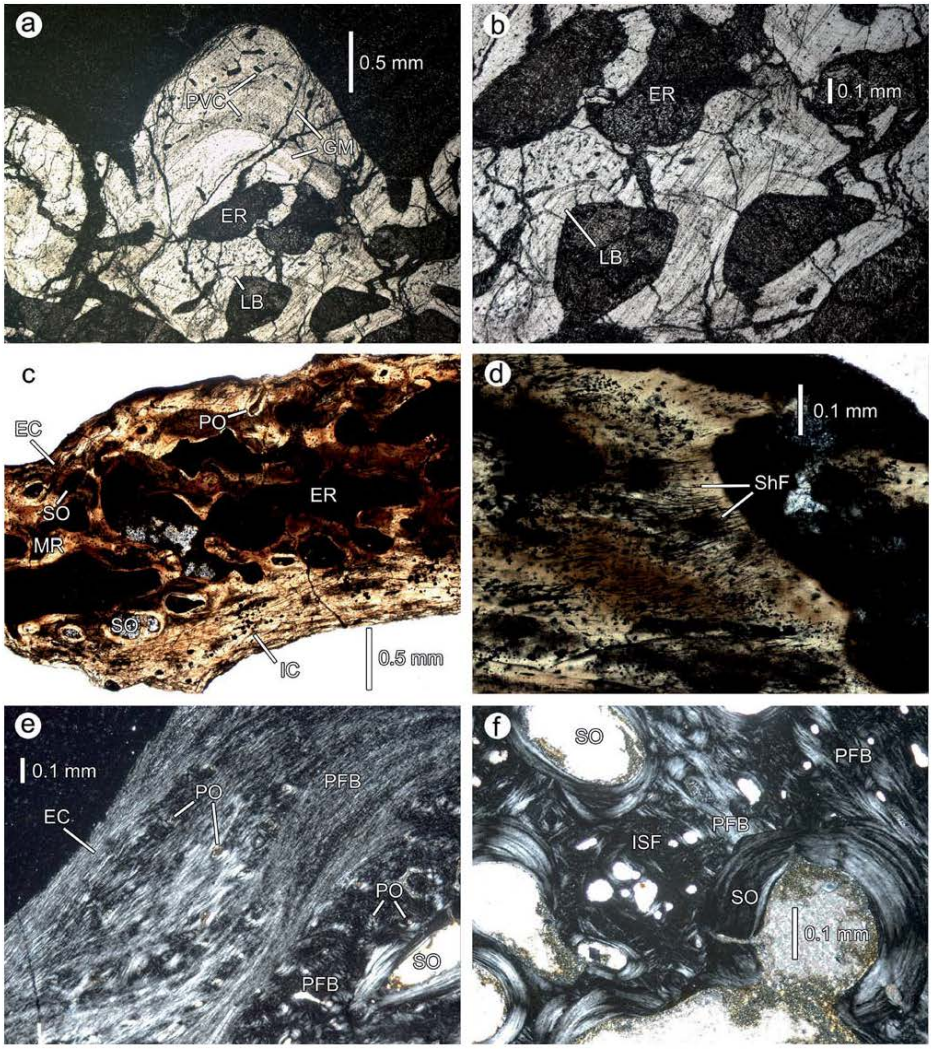

Fig. 7. a–b. *Sclerocephalus haeuseri* Goldfuss, 1847, SMNS 90517. Vertical section of postfrontal, reflected light. **a.** External cortex with external portion of middle region. **b.** Close up of middle region with large erosion rooms lined by secondary bone. **c–d.** *Archegosaurus decheni* Goldfuss, 1847, MB.Am.152. Vertical section of prefrontal. **c.** Histological overview in normal transmitted light. **d.** Close up of shelf for articulation with the lacrimal with horizontally oriented Sharpey's fibers in normal transmitted light. – **e–f.** *Kupferzellia wildi*, Schoch, 1997, SMNS 91247. Vertical section of ?supratemporal. **e.** External cortex with lateral part of sculptural saddle, polarized light. **f.** Middle region with secondary osteons, polarized light. – For abbreviations, see text.

tural fibers are present, in which most of the lacunae are round. Canaliculi are mostly short. More internally, the secondary osteons are smaller and aligned in two to four rows that are separated by avascular layers of parallel-fibered bone.

Internal cortex. Coarse parallel-fibered bone constitutes the bone matrix of the internal cortex, with locally changing directions of its fibers. Most of the bone cell lacunae are spindular and have few canaliculi. Extrinsic fibers are not visible. Vascularization is poor and consists of scattered primary vascular canals.

3.3.8. *Mastodonsaurus giganteus* (Temnospondyli, Stereospondylomorpha, Capitosauroidea)

The dermal sculpture of *Mastodonsaurus giganteus* (JAEGER, 1828) is composed of regular, rather square pits on the skull table. The peripheral parts of the bones of the postorbital skull table consist of radiating ridges and furrows. Some sections for this study were cut through bones with polygonal sculpture, and others were made perpendicular or parallel to the radiating ridges. The ratio external cortex : middle region : internal cortex is 1 : 3 : 0.4. The bone thickness of the investigated specimens ranges from 8 mm to 17 mm. Additionally, the clavicular blade of a small juvenile specimen has been sectioned and is described separately below.

External cortex. The bone matrix consists of both rather coarse parallel-fibered bone and fine interwoven structural fibers. In some saddles, more parallel-fibered bone is present than interwoven structural fibers, whereas in others, a matrix of interwoven structural fibers predominates (Fig. 8a). In the sculptural valleys, coarse parallel-fibered bone is generally (but not always) more common, and layers of interwoven structural fibers may be intercalated within the parallel-fibered bone. The bone cell lacunae in interwoven structural fibers are often irregular in outline and arrangement, and possess short or no canaliculi (Fig. 8b). Rather short, but thick Sharpey's fibers with a diameter of 25 to 28 µm are present in the sculptural saddles and are loosely arranged. Sharpey's fibers are less abundant in the sculptural valleys, and may also be absent. In some specimens, the external parts of the external cortex are poorly vascularized by isolated primary vascular canals and primary osteons, but more interiorly in the cortex, primary osteons are abundant and are aligned in rows or form an anastomosing network. In other specimens (SMNS 91252), almost the complete external cortex is well vascularized by primary vascular canals and especially primary osteons, which are arranged in a regular succession parallel to the external surface (Fig. 8c). In the more external part of the cortex, the canals are distinctly smaller than the canals in the more interior portion, and in the most external part, some of the canals have become larger again. These differences in vascularization between specimens might be explained as ontogenetic variation (see discussion). Isolated secondary osteons are present in the interlaced intermediate zone between external cortex and middle region. Growth marks are often conspicuous and follow the pattern of the external sculpture (Fig. 8d). In the external cortex of SMNS 91249, an almost horizontal line represents the former external bone surface in an earlier ontogenetic stage. More externally, three succeeding generations of sculptural saddles are visible that became increasingly steeper in ontogeny (Fig. 8e). External surface resorption and remodeling as described above for *Edops* and *Eryops* are present in some specimens (Fig. 9a). In SMNS 80878, the external cortex is in some areas extensively remodelled by secondary osteons that sometimes occur in clusters and may form Haversian tissue.

Middle region. This mostly coarse cancellous region is extensively vascularized by primary and secondary osteons (Fig. 9b), and large vascular spaces may occur in the more interior portion. These areas can be designated as trabecular with thick, short trabeculae, which are irregularly arranged. More externally and internally, in direction to the cortices, primary osteons are frequently arranged in rows, with less vascularized layers of bone intercalated between them. The secondary osteons form Haversian tissue in many areas (Fig. 9b, bottom). More externally, erosion rooms with Howship's lacunae are detectable (Fig. 8d, e).

The primary and secondary osteons course frequently approximately parallel to the radiating sculptural saddles. The interstitial primary bone consists mainly of parallel-fibered bone. Rather fine primary fibers are present that are oriented subparallel, but change their direction in succeeding, often irregular layers, similar to *Edops* and *Eryops* as described above. These fiber areas are remains of primary bone, which was remodelled and separated from secondary bone by resorption lines. In some areas or layers, primary fibers cross each other at approximately a right angle and form interwoven structural fibers. Bone cell lacunae in the fibrous areas are most often irregular in outline, whereas they are mostly spindular and possess branching canaliculi in the parallel-fibered bone.

Internal cortex. The internal cortex consists of less organized parallel-fibered bone whose fibers show an often irregular arrangement, and transitions to interwoven structural fibers exist. In the interior portion, primary vascular canals and primary osteons are arranged in rows and course mainly in the direction of radial sculpture (Fig. 9c). The more internal region is poorly vascularized. Thin extrinsic fibers (Sharpey's fibers) may extend obliquely into the bone.

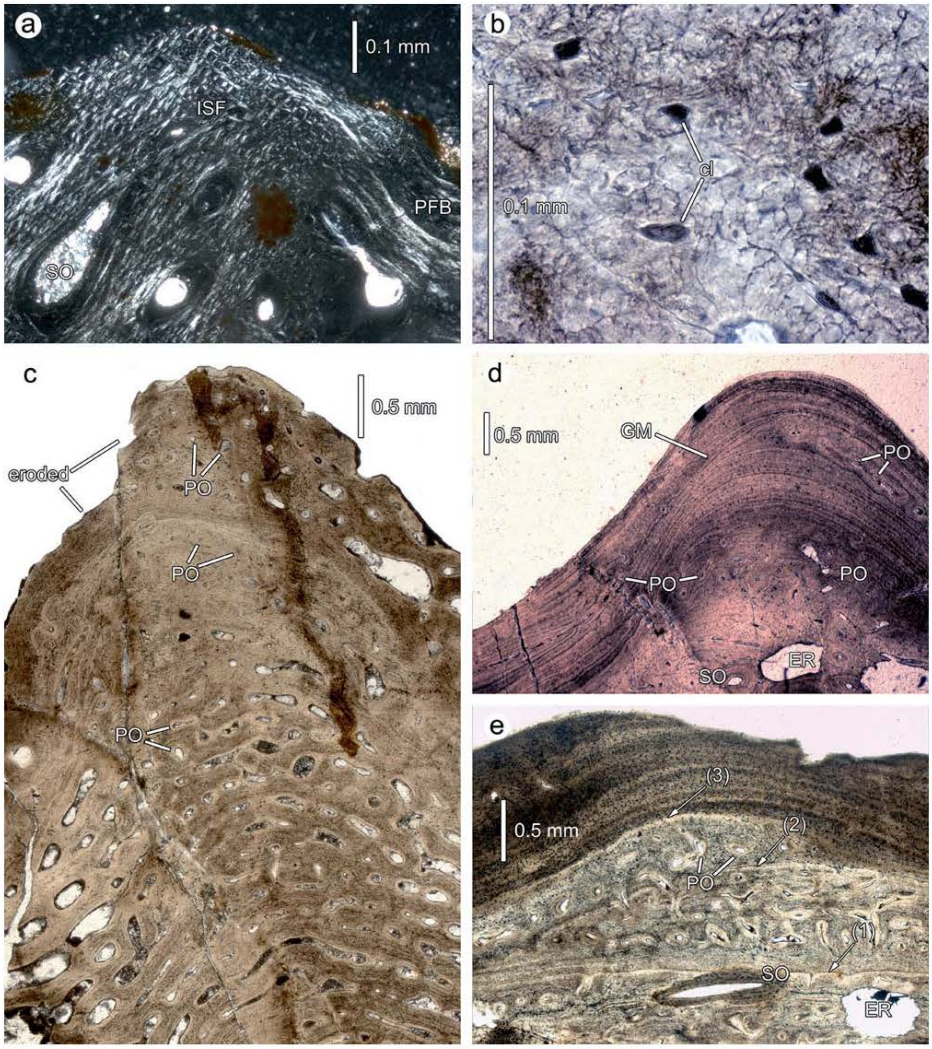

Fig. 8. *Mastodonsaurus giganteus* (JAEGER, 1828). Vertical sections of external cortex. – **a**. SMNS 91251. Slightly eroded sculptural saddle showing interwoven structural fibers. Polarized light. **b**. SMNS 91248. Bone cell lacunae in a matrix of interwoven structural fibers. **c**. SMNS 91252. Sculptural saddle with numerous primary osteons that are often arranged in a regular succession parallel to the external surface. **d**. SMNS 91248. Sculptural saddle showing growth marks; the more interior portion is well vascularized. **e**. SMNS 91248. The former bone surfaces of three succeeding generations of a sculptural saddle are visible; the first is almost horizontally aligned. – For abbreviations, see text.

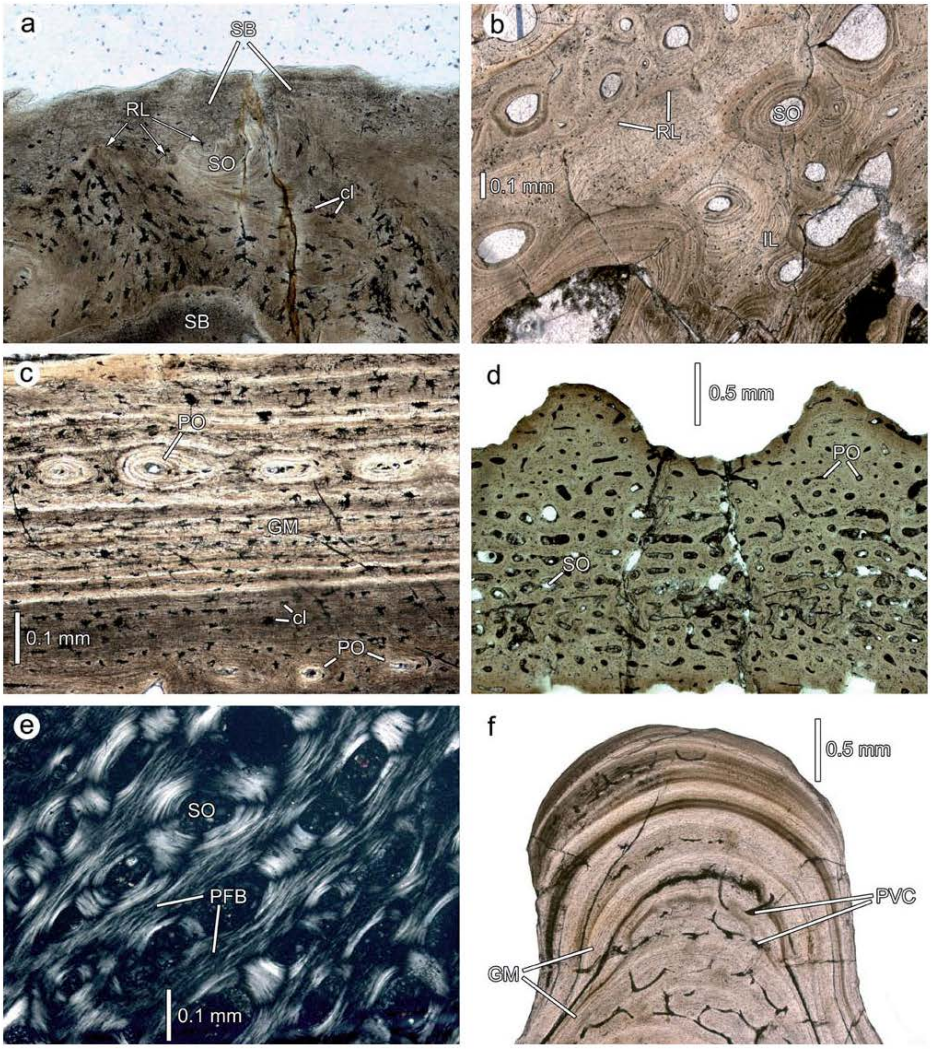

Fig. 9. **a**–**e**. *Mastodonsaurus giganteus* (JAEGER, 1828). **a**. SMNS 80878. Vertical section parallel to a sculptural ridge showing structures of surface resorption. **b**. SMNS 91248. Middle region in normal transmitted light, vertical section. Zone of extensive remodeling and Haversian tissue. **c**. SMNS 91248. More interior part of internal region with primary osteons in rows. **d**–**e**. Juvenile specimen, SMNS 91255. Interclavicle, vertical section transverse to the sculptural ridges. – **d**. Histological overview, normal transmitted light. **e**. The fine to coarse cancellous middle region with a matrix of coarse parallel-fibered bone, polarized light.
f. *Metoposaurus diagnosticus* (VON MEYER, 1842), MB.Hi.1719. Sculptural saddle of an unidentified dermal bone in normal transmitted light. – For abbreviations, see text.

3.3.9. Clavicular blade of a small juvenile specimen of *Mastodonsaurus giganteus*

The section is aligned transversely to the radiating sculptural ridges of this approximately 2.1 mm thick bone. The cortices are so extensively vascularised that they resemble closely the middle region. Therefore, it is no more appropriate to speak of a clear diploë structure, in contrast to the ontogenetically more advanced specimens. The determination of boundaries between the cortices and the middle region is thus rather arbitrary.

External cortex. The external cortex is highly vascularized by numerous, anastomosing primary vascular canals and primary osteons (Fig. 9d). Also few secondary osteons can be observed. There is no difference in the degree of vascularization and nature of the bone tissue between saddles and valleys. Growth marks are not visible. The primary bone tissue consists of coarse, poorly organized parallel-fibered bone that may fray out in fibers with changing direction. Interwoven structural fibers and Sharpey's fibers are not visible in the material under study. Most bone cell lacunae are randomly arranged, irregular in shape and possess few or no canaliculi.

Middle region. This fine to coarse cancellous region is distinguished from the cortices by the slightly larger diameter of many of its vascular canals, and the presence of several secondary osteons that may anastomose. Haversian tissue is not present. The rather small osteons are frequently arranged in layers (Fig. 9e). Few slightly larger erosion rooms without lining of lamellar bone are present. The interstitial primary tissue consists mainly of coarse, less organized parallel-fibered bone (Fig. 9e). In the primary bone matrix, the longitudinal axes of the spindular bone cell lacunae are directed parallel to the bone fibers. Canaliculi are hardly visible.

Internal cortex. The internal cortex is composed of coarse parallel-fibered bone. It is well vascularized by primary vascular canals and primary osteons that may anastomose (Fig. 9d). The bone cell lacunae are ordered and spindular with few canaliculi.

3.3.10. *Metoposaurus diagnosticus* (Temnospondyli, Stereospondylomorpha, Trematosauroidea)

It is not clear if the slides investigated here from *Metoposaurus diagnosticus* (VON MEYER, 1842) are derived from the skull roof or the dermal pectoral girdle. The ratio external cortex : middle region : internal cortex is 1 : 1.5 : 0.3. However, the middle region has collapsed by the superimposed load of sediment in the specimens under study and was therefore originally probably somewhat thicker. The bone investigated attains a thickness of 9 mm.

External cortex. The more interior part of the cortex is well vascularized by numerous, partially anastomosing primary vascular canals of mostly a small diameter, whereas the number of canals decreases in direction to the external bone surface and the top of the saddles (Fig. 9f). The bone matrix is composed of homogeneous parallel-fibered bone and shows several distinct growth marks that allow to trace the growth of the rather steep sculptural saddles. Numerous bone cell lacunae are visible that appear mostly irregular-elongate in shape. Poor preservation precludes recognition of canaliculi. In the sculptural saddles, the Sharpey's fibers are arranged in clusters that are mostly present in the lateral parts of the saddles (Fig. 10a), where they are oriented interiorly and medially. In the sculptural valleys, the clusters are more densely arranged and extend deep into the cortex (Fig. 10a). The diameter of the fibers amounts 17 to 25 µm.

Middle region. The external cortex grades into the coarse cancellous middle region with numerous secondary osteons that may form Haversian tissue. The primary bone matrix is represented by fine, homogeneous parallel-fibered bone.

Internal cortex. The internal cortex is thin compared to the middle and external region and consists of homogeneous parallel-fibered bone that is largely avascular (Fig. 10b). It can be distinguished from the middle region by a distinct transition zone.

3.3.11. *Plagiosuchus pustuliferus* (Temnospondyli, Stereospondylomorpha, Plagiosauridae)

For the present study, a dermal bone fragment of *Plagiosuchus pustuliferus* (FRAAS, 1896) (SMNS 82023), which derives probably from the skull roof and bears a sculpture of tubercles and low ridges between them, was sectioned. The bone thickness amounts 11 mm. In this fragment, the cortices are highly vascularized similar to the middle region, and thus a diploë structure is not visible. The determination of external cortex, middle region, and internal cortex in the following is somewhat arbitrarily and based on the higher density of vascular canals in the middle region and the presence of extrinsic fibers (Sharpey's fibers) in the cortices. The vascularization is slightly less well developed in the external cortex of MB.Hi.1705 (maximum bone thickness 4 mm), a slide of an unidentified dermal bone of *Plagiosuchus*, than in that of SMNS 82023. Nevertheless, a clear diploë structure is not developed also in MB.Hi.1705.

External cortex. The complete external cortex is well vascularized by numerous, partially anastomosing primary vascular canals and primary osteons in SMNS 82023, whereas in MB.Hi.1705, the external portion of the cortex is nearly avascular. Densely arranged Sharpey's

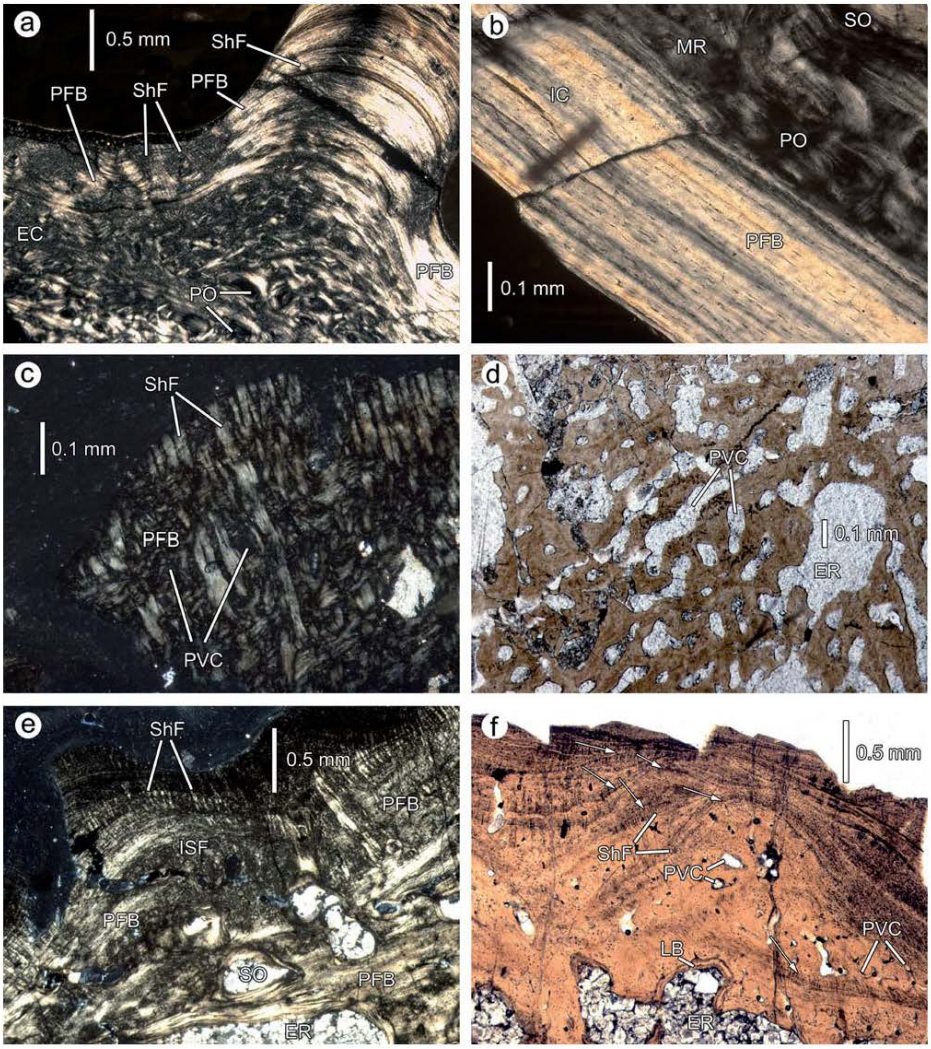

Fig. 10. a–b. *Metoposaurus diagnosticus* (VON MEYER, 1842), vertical sections through unidentified dermal bone. **a.** MB.Hi.1720. Sculptural saddle and external cortex in polarized light. **b.** MB.Hi.1721. Internal cortex in polarized light. – **c–d.** *Plagiosuchus pustuliferus* (FRAAS, 1896), SMNS 82023. Vertical section through fragment of dermal skull roof. **c.** Sculptural saddle with Sharpey's fibers in polarized light. **d.** Middle region with primary vascular canals and erosion rooms, normal transmitted light. – **e–f.** *Plagiosternum granulosum* (FRAAS, 1889), SMNS 91256. Vertical section of interclavicle. **e.** Sculptural saddle and valley with Sharpey's fibers and external part of middle region, polarized light. **f.** External cortex with eroded surface, showing sculptural saddles of different generations (indicated by arrows) and Sharpey's fibers both in saddles and valleys, normal transmitted light. – For abbreviations, see text.

fibers penetrate the external region both in the sculptural saddles and valleys (Fig. 10c) and extend far interiorly within the cortex. The fibers have a diameter of mostly 22 to 26 µm and may ramify in two or three branches. The largest part of the bone tissue consists of coarse parallel-fibered bone with a more irregular fibrous arrangement. Spindle-shaped bone cell lacunae are present that possess branching canaliculi. In some areas, especially the sculptural saddles, also islets of interwoven structural fibers are discernable. Cyclic growth marks are not continuous and have an indistinct appearance in SMNS 82023, whereas they are more distinct in the external part of the external cortex in MB.Hi.1705.

Middle region. This coarse cancellous region is extensively vascularized by primary vascular canals and primary osteons, and isolated, medium-sized erosion cavities are present (Fig. 10d). Some of them show Howship's lacunae, and secondary lamellar bone lining is absent in the SMNS specimen under study, whereas in MB.Hi.1705, scattered, small secondary osteons are discernable. The bone matrix consists in large parts of interwoven structural fibers, and also parallel-fibered bone is present.

Internal cortex. The bone matrix consists mostly of poorly organized parallel-fibered bone. Sharpey's fibers are present that are shorter and distinctly thinner than those of the external cortex. Vascularization is well developed and consists of numerous primary vascular canals that are often aligned in rows or may anastomose.

3.3.12. *Plagiosternum granulosum* (Temnospondyli, Stereospondylomorpha, Plagiosauridae)

A fragment of an interclavicle of *Plagiosternum granulosum* (Fraas, 1889) (SMNS 91256) with polygonal sculpture was sectioned that has a maximum thickness of 11 mm. Additionally, the vertical section of an unidentified, 7 mm thick dermal bone of *Plagiosternum* (MB. Hi.1714) was investigated. The ratio external cortex : middle region : internal cortex is 1 : 2.9 : 0.8.

External cortex. The external cortex is composed of coarse, poorly ordered parallel-fibered bone, and islets of interwoven structural fibers can be found especially in the more internal regions of the sculptural saddles and in the interior parts of the cortex (Fig. 10e). The bone cell lacunae in the parallel-fibered bone are of irregular shape with moderately long canaliculi. In the SMNS specimen, Sharpey's fibers are densely arranged in both the sculptural saddles and in the valleys, comparable to the situation in *Plagiosuchus*. The diameter of the Sharpey's fibers varies between 17 to 26 µm, and most of them terminate in approximately the external half of the external region. Zones and annuli are well visible and delineate sculptural saddles of earlier generations, in which Sharpey's fibers are visible (Fig. 10f). The external cortex of the SMNS specimen is moderately vascularized in its interior portion by primary vascular canals, whereas the external portion is largely avascular (Fig. 10f). In MB.Hi.1714, the complete cortex is well vascularized by anastomosing primary canals whose diameters decrease in size in the more external portion of the cortex (Fig. 11a). The difference in the degree of vascularization between the Berlin and the Stuttgart specimen might be explained as ontogenetic variation (see discussion).

Middle region. A rather small transition zone between the external cortex and the middle region is characterised by scattered secondary osteons. The middle region was extensively affected by remodeling. It is characterised by large erosion rooms that are separated by long, irregularly arranged trabeculae of varying thickness (Fig. 11b). Some erosion rooms are lined by secondary lamellar bone. The primary bone matrix within the trabeculae consists of well-ordered parallel-fibered bone with spindular bone cell lacunae.

Internal cortex. The bone tissue is composed of parallel-fibered bone with often irregularly arranged fibers, and transitions to interwoven structural fibers are locally present. Sharpey's fibers that are distinctly thinner than those of the external region penetrate the internal cortex obliquely at an angle of about 60° and are densely arranged. Primary vascular canals that may anastomose are more numerous in the interior than in the internal part of the cortex. Cyclic growth marks are well visible (Fig. 11c).

3.3.13. *Gerrothorax* sp. (Temnospondyli, Stereospondylomorpha, Plagiosauridae)

The thin sections were prepared from bone fragments of the interclavicle and clavicle, ranging from 3.3 mm to 9 mm in thickness. The dermal sculpture is tubercular, and low sculptural ridges may connect the tubercles. The ratio external cortex : middle region : internal cortex is 1 : 1.9 : 0.9.

External cortex. The interior portion of the external cortex is moderately to highly vascularized by primary vascular canals and primary osteons that often branch and anastomose, whereas vascularization is low in the external portion of the cortex (Fig. 11d). The sculptural valleys and the lateral parts of the saddles consist mainly of fine to coarse parallel-fibered bone in which the bone cell lacunae are often spindular with moderately long to long canaliculi. The interior parts of the sculptural saddles, in contrast, show general isotropy under polarized light, and the bone cell lacunae are rather round and haven often long, branching canaliculi. The isotropy can probably be attributed to the superposition of the Sharp-

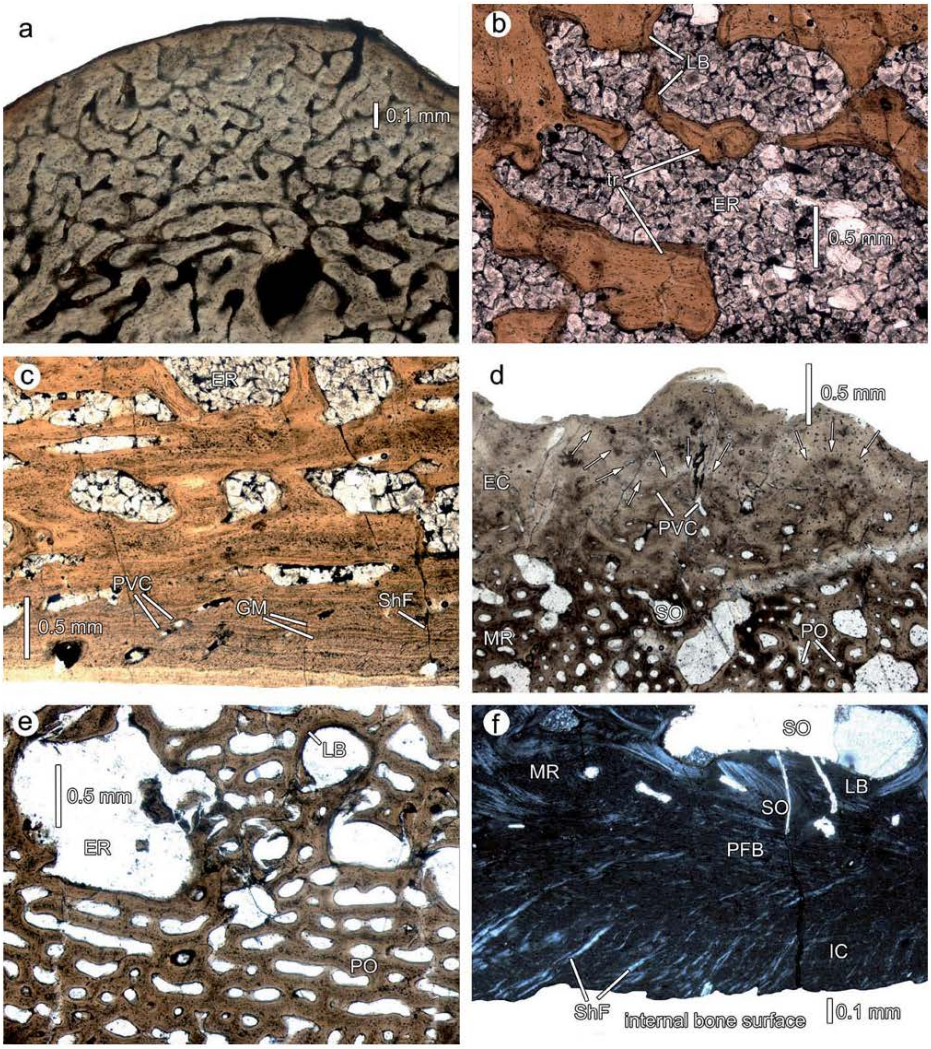

Fig. 11. **a**–**c**. *Plagiosternum granulosum* (FRAAS, 1889). **a**. MB.Hi.1714. Vertical section of unidentified dermal bone, sculptural saddle, normal transmitted light. **b**–**c**. SMNS 91256. Vertical section of interclavicle. **b**. Middle region showing trabecular structure with large erosion rooms. **c**. Internal cortex in normal transmitted light. – **d**–**f**. *Gerrothorax* sp. **d**. SMNS 91258. Vertical section of clavicle, histological overview of external cortex and middle region in normal transmitted light; the arrows indicate the bone surface of a former generation. **e**. SMNS 91257. Vertical section of clavicle in polarized light, showing the middle region with numerous primary osteons and larger erosion rooms. **f**. SMNS 83033. Vertical section of interclavicle, internal cortex in polarized light; note the oblique Sharpey's fibers penetrating the bone. – For abbreviations, see text.

ey's fibers in the cores of the saddles. In some regions more interior in the cortex, the bone tissue may show transitions to diagonally arranged interwoven structural fibers of irregular size. Rather thin Sharpey's fibers with a diameter of 8 to 11 µm, that are not as densely arranged as in *Plagiosuchus* and *Plagiosternum*, are visible in the sculptural tubercles and are fewer in number in the valleys. Cyclic growth marks are present in the external cortex. In one interclavicle (SMNS 83033), a former generation of sculptural saddles is visible in the interiormost part of the external cortex (Fig. 11d). These old sculptural saddles are distinctly smaller and the valleys narrower than those of the actual external surface.

Middle region. The transition zone from the external cortex to the middle region is rather thin and bears scattered secondary osteons. In most specimens, the middle region varies from coarse cancellous to trabecular (Fig. 11e). In some areas, numerous primary osteons predominate and may be arranged in rows, whereas in other areas, scattered, large erosion rooms prevail, that are separated by irregularly arranged trabeculae. In some parts, remodeling was so extensive that Haversian tissue was formed (Fig. 11f, on top). The primary tissue is parallel-fibered bone, but also a matrix of interwoven structural fibers that are diagonally arranged with respect to the bone surface occurs, whose sparse bone cell lacunae are mostly round and bear no or only short canaliculi.

Internal cortex. The internal cortex is composed of coarse, less ordered parallel-fibered bone. Rather loosely arranged Sharpey's fibers of varying size extend into the internal region at an oblique angle (30–50°), some of them extending until to the middle region (Fig. 11f). Only very few primary vascular canals are visible. These are mostly situated more interiorly in the internal cortex and course parallel to the internal bone surface.

3.3.14. *Diplocaulus magnicornis* (Lepospondyli, Nectridea)

The sectioned bone fragments of *Diplocaulus magnicornis* Cope, 1882, ranging from 7 mm to 14 mm in thickness, represent lateral parts of the conspicuous 'horns' of this nectridean, so that a sculptured compact cortex encloses the middle region dorsally, laterally, and ventrally. Therefore, in the following, the cortex will be referred to as 'external cortex' only. The external cortex is much reduced with respect to the extensive middle region, the ratio external cortex : middle region : external cortex is 1 : 11.1 : 1. The dermal sculpture is composed of rounded polygons.

External cortex. The externalmost portion of the rather thin cortex is for the largest part avascular with very few, small primary canals, whereas its more interior part is well vascularized by primary canals and primary osteons. In a transitional region between cortex and middle region, several small erosion rooms and primary and secondary osteons are present (Fig. 12a). The bone matrix of the cortex consists largely of coarse parallel-fibered bone (Fig. 12b), and Sharpey's fibers are restricted to the sculptural saddles, where their arrangement is moderately dense. The fibers have a comparatively small diameter of 11 to 13 µm. The cores of many sculptural saddles show isotropy under polarized light; as outlined for *Gerrothorax* (see above), this might be attributed to superposition of the Sharpey's fibers. In most specimens, interwoven structural fibers constitute the predominant matrix in the more interior part of the external cortex (Fig. 12c). In the parallel-fibered bone, the cell lacunae have often long, branching canaliculi and are most often spindular (in the valleys) and rounded (in the saddles). The cell lacunae within the interwoven structural fibers, in contrast, are irregular in shape and have often no or only stumpy canaliculi. Throughout the external cortex, growth marks are present that are continuous in saddles and valleys and follow their relief.

Middle region. The middle region of *Diplocaulus* is highly porous and strongly affected by successive resorption and reconstruction of bone. Thin, long trabeculae that are mostly orientated in a dorsoventral and horizontal direction enclose rectangular shaped bone cavities of similar size (Fig. 12d). The ordered appearance of trabeculae and cavities is unique among the basal tetrapods studied here. Most of the cavities have a thin covering of secondary lamellar bone (Fig. 12e). In the more external cavities, the lining of lamellar bone is frequently absent. The primary bone tissue consists in large parts of coarse parallel-fibered bone, but also areas with interwoven structural fibers do exist. Partially cut primary osteons can be discerned in the primary tissue of the trabeculae.

Specimen MCZ 2269-3 provides interesting data concerning the extensive resorption and remodeling of the middle region. Structures of resorption are visible both in the primary matrix and the secondary lamellae (Fig. 12f). The primary bone matrix exhibits cyclical growth marks, with the different zones being delimited by distinct growth lines. The secondary lamellae surround the zones of primary bone matrix continuously, indicating their deposition after the formation of the zones.

3.3.15. *Pantylus cordatus* (Lepospondyli, 'Microsauria')

A small, 3 mm thick fragment of the dermal skull roof of *Pantylus cordatus* Cope, 1881 consisting of one sculptural saddle and one valley plus parts of the middle region was sectioned. *Pantylus* has a pronounced polygonal sculpture on its dermal skull roof. The internal cortex and

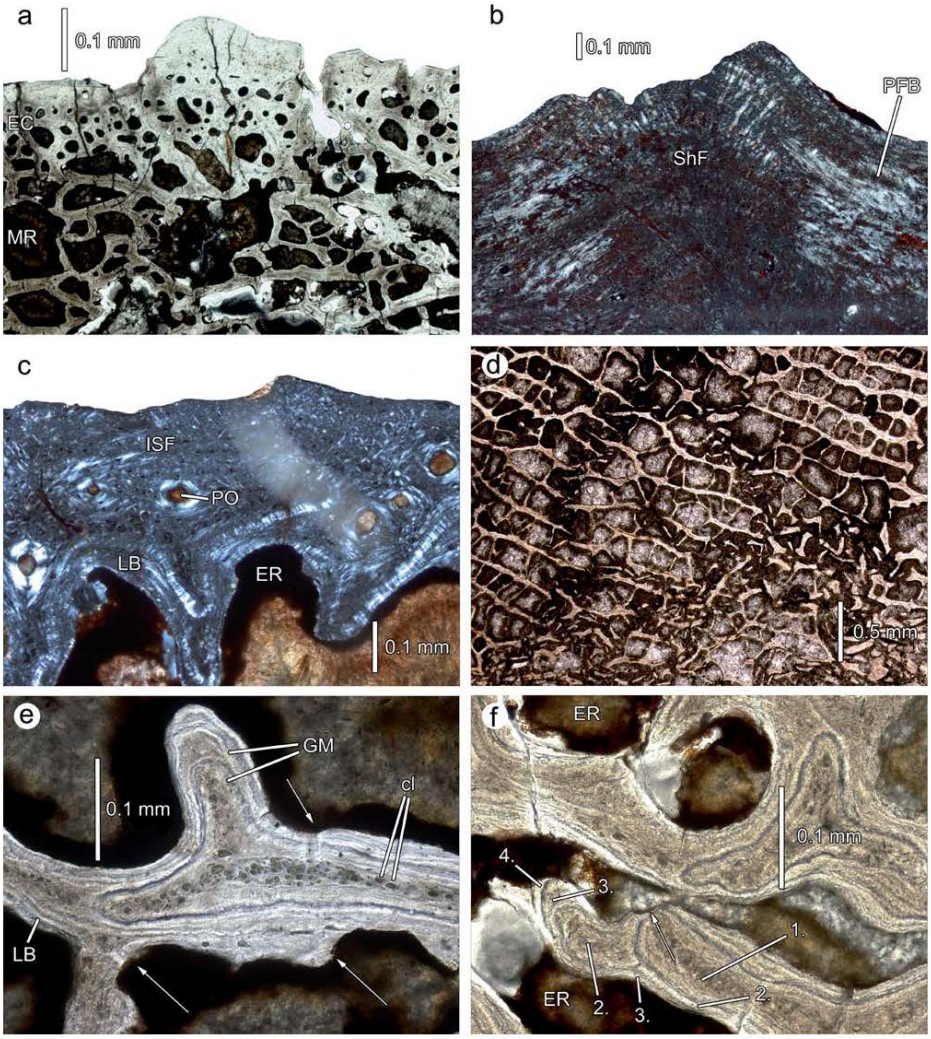

Fig. 12. *Diplocaulus magnicornis* Cope, 1882. Vertical sections of the 'cheek'-region. – **a**. UCMP 203658. Histological overview of external cortex with middle region in normal transmitted light. **b**. UCMP 203505. Sculptural saddle (partially eroded) in polarized light showing fan-shaped Sharpey's fibers and matrix of parallel-fibered bone. **c**. UCMP 203658. Interior part of external cortex (the more external part is eroded) with erosion rooms of the middle region. **d**. MCZ 2269. Overview of the trabecular middle region in normal transmitted light. **e**. UCMP 203658. Trabeculae of the middle region in normal transmitted light, resorptive structures are indicated by arrows. **f**. MCZ 2269. Trabeculae of middle region in normal transmitted light, the numbers 1–4 indicate the order of bone deposition, the arrow marks a resorptive structure. – For abbreviations, see text.

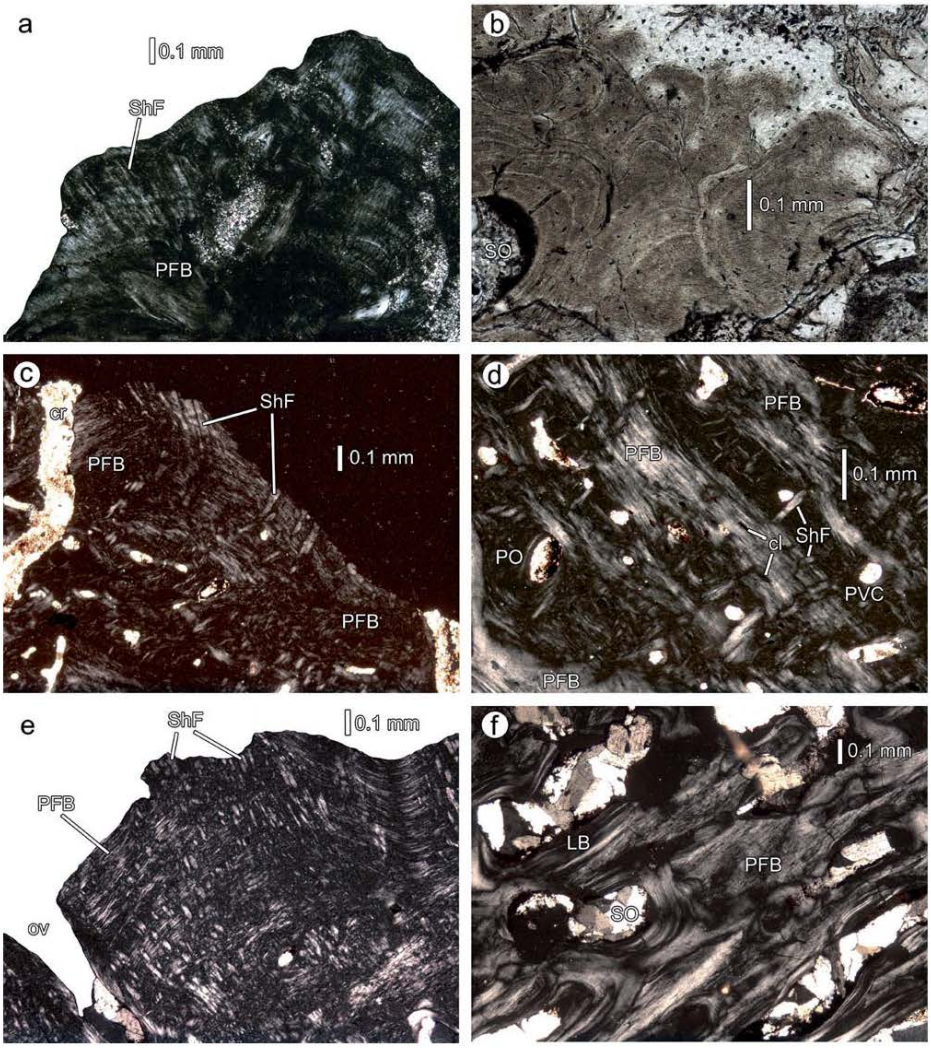

Fig. 13. **a**–**b**. *Pantylus cordatus* Cope, 1881, UCMP 20296. Vertical section of dermal skull fragment. **a**. Sculptural saddles in polarized light. **b**. Transitional zone between external cortex and middle region in normal transmitted light, showing extensive bone remodeling.– **c**–**d**. *Seymouria baylorensis* Broili, 1904. MCZ without number. Vertical section of ?angular. **c**. Sculptural saddle in polarized light. **d**. More interior portion of external cortex. – **e**–**f**. *Labidosaurus hamatus* Cope, 1895, MCZ without number. Vertical section of skull table bone. **e**. Sculptural saddle with adjacent sculptural valleys in polarized light, a vascular canal opens in the valley on the left. **f**. Middle region with secondary osteons in polarized light. – For abbreviations, see text.

the more internal part of the middle region of this specimen are eroded.

External cortex. Densely arranged Sharpey's fibers penetrate the high, steep sculptural saddles (Fig. 13a). The diameter of the fibers varies between 13 and 21 µm. The primary bone matrix consists of parallel-fibered bone. The sculptural valley is diagenetically altered so that the original bone matrix cannot be discerned, and it cannot be stated if Sharpey's fibers were present. The vascularization of the external cortex is low with scattered primary vascular canals and primary osteons. On the left side of the sculptural saddle, a conspicuous resorption line is visible, similar to the situation described for *Edops*, *Eryops* and *Mastodonsaurus* (see above). Here, surface erosion with formation of secondary bone including a secondary osteon has taken place. The bone cell lacunae in the primary bone tissue are round throughout with no or short canaliculi. In the secondary bone tissue, the lacunae are larger, more numerous, and have longer canaliculi. Cyclic growth marks that follow the external sculpture are visible, but are absent in the remodelled area.

Middle region. The transitional zone between the external cortex and the middle region is still rather compact with scattered secondary osteons and several, 'chaotic' resorption lines, indicating that this region underwent extensive remodeling (Fig. 13b). In the middle region, the erosion cavities become larger and constitute extensive spaces, so that this region can be designated as trabecular. The cavities are bounded by thick, irregularly arranged trabeculae that may be covered by secondary lamellar bone. The primary bone matrix consists mostly of coarse, less ordered parallel-fibered bone.

3.3.16. *Seymouria baylorensis* (Seymouriamorpha)

From *Seymouria baylorensis* Broili, 1904, a small dermal bone fragment of the lower jaw, probably the angular, was studied. The 5.5 mm thick bone was sectioned perpendicular to the sculptural ridges. The ratio external cortex : middle region : internal cortex is 1 : 2.7 : 0.9.

External cortex. The bone tissue comprises mostly poorly organized parallel-fibered bone (Fig. 13c). Bone cell lacunae appear spindular or round, depending on their orientation (see below), and have moderately long to long, branching canaliculi. In the interior portion of the cortex, layers of fine parallel-fibered bone are present, whose fibers are cut roughly longitudinally (with spindular cell lacunae) and brighten up in polarized light. They alternate with those whose fibers are cut transversely (with round bone cell lacunae) and remain dark in polarized light, so that the bone is reminiscent of an isopedine-like tissue (Fig. 13d). Scattered Sharpey's fibers that may bifurcate penetrate the sculptural saddles. They are of different length and measure 21 to 32 µm in diameter. Compared e. g. to *Eryops* or *Plagiosuchus* (see above), they are rather loosely arranged. The Sharpey's fibers are only sporadically present in the sculptural valleys. The interior portion of the cortex is moderately to highly vascularized by primary canals and primary osteons. In the external portion of the external cortex, however, vascularization is low and consists of isolated primary canals.

Middle region. This region is fine to coarse cancellous and is characterized by scattered secondary osteons of varying orientation. They may possess wide Haversian canals. The primary bone matrix consists of homogeneous parallel-fibered bone.

Internal cortex. The internal cortex is composed of parallel-fibered bone. It is well vasularized by different layers of primary vascular canals and primary osteons.

3.3.17. *Labidosaurus hamatus* (Amniota, Eureptilia, Captorhinidae)

Many parareptiles and basal eureptiles possess distinctly sculptured dermal bones, similar to those of temnospondyls (Kissel et al. 2002; Modesto et al. 2007; Witzmann, unpublished data). From the captorhinid *Labidosaurus hamatus* Cope, 1895, a 5 mm thick bone fragment of the skull table with a reticular sculpture has been sectioned. The internal cortex is eroded in this specimen.

External cortex. This region is mainly composed of coarse parallel-fibered bone (Fig. 13e). The majority of the well mineralized, long Sharpey's fibers can be found in the sculptural ridges, whereas the sculptural valleys are nearly devoid of them. The diameter of most Sharpey's fibers varies between 16 and 29 µm. Vascularization is low and consists of scattered simple primary canals and primary osteons in the interior portion of the external cortex, whereas the external portion is almost avascular.

Middle region. The middle region is coarse cancellous and is populated by numerous secondary osteons that course in different directions (Fig. 13f). Locally, Haversian tissue is formed. Mostly fine, homogenous parallel-fibered bone constitutes the primary bone matrix. The bone cell lacunae are generally elongate. Canaliculi are not visible, probably due to poor preservation.

The histological features of the investigated taxa are summarized in Tables 2–4.

4. Discussion

4.1. Growth of bony tubercles and ridges, and remodeling of the outer bone surface

Among extant tetrapods, growth of dermal bony tubercles and ridges has been studied in the osteoderms of squamates and in dermal skull bones and osteoderms of crocodiles. In squamates, the presence of pits and ridges on the external surface of osteoderms follows from both local resorption and growth of bone (ZYLBERBERG & CASTANET 1985; LEVRAT-CALVIAC & ZYLBERBERG 1986), whereas in crocodile dermal bones, DE BUFFRÉNIL (1982) stated that sculpture is mainly the result of local resorption. In contrast, VICKARYOUS & HALL (2008) found no evidence for morphogenesis of bone sculpture by resorption in *Alligator mississippiensis* and presumed that sculptural ridges develop by preferential bone growth. Concerning basal tetrapods, BYSTROW (1935, 1947) showed that the development of bone sculpture in the temnospondyls *Benthosuchus*, *Platyoposaurus* and *Dvinosaurus* took place solely by growth of the bony ridges and tubercles, and resorptive processes were not involved.

The thin sections of the dermal bones of skull and pectoral girdle in the basal tetrapods investigated here corroborate BYSTROW's findings and show that the dermal sculpture did not develop by local resorption of the bone surface, comparable to the pattern in basal tetrapod osteoderms (WITZMANN & SOLER-GIJÓN 2008). The growth marks follow clearly the pattern of sculptural saddles and valleys. In general, the sculptural saddles in basal tetrapods are characterized by a much greater number of Sharpey's fibers than the valleys (see below). The presence of these anchoring fibers can induce preferential growth of the mineralized tissue or bone around them (BOYDE 1972; SIRE 1985, 1986; MOWBRAY 2005), and this might have contributed to the formation of the bony tubercles and ridges that constitute the dermal sculpture in basal tetrapods (see also WITZMANN & SOLER-GIJÓN 2008). Nevertheless, resorptive structures are visible on the bone surface in the sculptural saddles in some taxa: the better vascularized secondary bone lies discordantly on the primary bone and is separated from it by a distinct resorption line that is often interiorly convex. Very similar cases of remodeling in the external cortex have been reported by SCHEYER & SÁNCHEZ-VILLAGRA (2007) in the shell bones of two turtle taxa, the extant *Podocnemis erythrocephala* (SPIX, 1824) and the fossil *Taphrosphys sulcatus* (LEIDY, 1856), where this phenomenon is interpreted as a reaction of bone to infection or trauma. The remodeling structures on the bone surface in the basal tetrapods investigated here might result from similar reasons and can be regarded as unusual bone growth that did not contribute to the formation of dermal bone sculpture.

The fact that morphogenesis of bony ridges and tubercles took place by preferential growth in all investigated taxa of basal tetrapods strongly suggests that dermal sculpture evolved once in the finned stem-tetrapods after the reduction of the dermal components (odontodes) and was basically retained in all lineages of basal tetrapods including early amniotes (see below).

4.2. Vascularization of the external and internal cortex

BYSTROW (1935, 1947) found a network of capillaries in the external cortex of the stereospondyls *Benthosuchus* and *Wetlugasaurus* that he named the 'rete vasculosum'. He suggested that this network carried blood capillaries into the overlying dermis. In the temnospondyls *Platyoposaurus* and *Dvinosaurus*, and in the seymouriamorph *Enosuchus*, the same author found this network to be absent and the cortex rather avascular. For BYSTROW (1947), this finding was of great palaeobiological significance. He called those forms that possess the 'rete vasculosum' the 'hydrophilous labyrinthodonts' and concluded that they were water-dwellers that breathed primarily through their wet skin; in contrast, those basal tetrapods in which this network is absent were considered as 'xerophilous labyrinthodonts' that lived mainly terrestrially and relied primarily on lung-breathing rather than on cutaneous respiration, since the integument was interpreted to be less vascularized. BYSTROW (1947) regarded the temnospondyl *Dvinosaurus* as an exception since it lived aquatically and lacks the 'rete vasculosum'. This discrepancy, however, was explained by the fact that *Dvinosaurus* possessed gills throughout its lifetime and therefore, cutaneous respiration was not necessary for gas exchange (BYSTROW 1947).

The thin sections of basal tetrapod dermal bones investigated here show that the external cortex varies in the density of vascularization (Tab. 2). In taxa such as the presumably semi-terrestrial *Edops*, *Chenoprosopus* and *Eryops*, and the rather terrestrial *Acheloma*, *Pantylus* and *Labidosaurus*, the external cortex is poorly vascularized or almost avascular. In most other taxa investigated, a moderate to high number of primary vascular canals is present in the more interior part of the cortex where they may anastomose and form a 'rete vasculosum' sensu BYSTROW (1935, 1947). However, there is a drop in vascularization towards the bone surface, and thus the more external portion of the cortex is populated by sparsely distributed primary canals, or the bone is even avascular. In some specimens of the aquatic *Mastodonsaurus*, the external cortex is throughout well vascularized by primary canals and even more by primary osteons that are arranged in layers and may anastomose. Towards the external surface of the bone, however, many of the canals get

Tab. 2. Summary of histological data concerning the external cortices of the dermal bones investigated. ** indicates that the Sharpey's fibers are not mineralized. Abbreviations: int., interior; mod., moderate. For further abbreviations, see text.

Taxon	Bone tissue	Vascularization	Sharpey's fibers		Growth marks
			Ø in µm	density	
Porolepiform and stem-tetrapods					
Laccognathus	fine PFB, odontodes	high	2**	loose	not visible
Panderichthys	fine PFB	moderate	5 6	mod. dense	not visible
Acanthostega	fine to coarse PFB	mod. to high	3 5	loose	not visible
Greererpeton	coarse PFB	mod. to high	3 7	loose	not visible
Temnospondyls					
Edops	coarse PFB > ISF	low	21	mod. dense	distinct
Chenoprosopus	coarse PFB > ISF	low	8 17	dense	distinct
Eryops	coarse PFB > ISF	low	21 29	dense	distinct
Acheloma	fine PFB	low	15 31	dense	weak
Sclerocephalus	?	moderate to low	?	?	distinct
Archegosaurus	fine PFB	mod. to high (int.)	?	?	not visible
Kupferzellia	coarse PFB > ISF	moderate (int.)	5 16	loose	weak
Mastodonsaurus	coarse PFB, ISF	mod. to high	25 28	loose	distinct
Mastodonsaurus (juv.)	coarse PFB	high	?	?	not visible
Metoposaurus	fine PFB	mod. to high (int.)	17 25	mod. dense	distinct
Plagiosuchus	coarse PFB > ISF	mod. to high	22 26	dense	distinct
Plagiosternum	coarse PFB > ISF	mod. to high (int.)	17 26	dense	distinct
Gerrothorax	fine /coarse PFB > ISF	mod. to high (int.)	8 11	mod. dense	distinct
Lepospondyls					
Diplocaulus	coarse PFB, ISF	high (int.)	11 13	mod. dense	distinct
Pantylus	fine PFB	low	13 21	dense	distinct
Seymouriamorpha					
Seymouria	coarse PFB	mod. to high (int.)	21 32	loose	not visible
Eureptilia					
Labidosaurus	coarse PFB	low	16 29	mod. dense	not visible

distinctly smaller in their diameter. A similar pattern is also visible in the Berlin specimen of the aquatic *Plagiosternum* (MB.Hi.1714). The fact that the primary vascular canals that may or may not form a network are mostly restricted to the more interior portion of the cortex renders a connection between cutaneous respiration and vascularization of the bone doubtful. Furthermore, even when the canals extend to the external portion of the cortex and to the bone surface as in the mentioned specimens of *Mastodonsaurus* and *Plagiosternum*, they constitute a very irregular and thus less effective route for the blood to reach the soft-tissue integument, as correctly pointed out by Coldiron (1974).

The primary vascular canals in the external cortex rather had the function to supply the bone during its growth. Their varying density, presence or absence might be explained with different growth rates in bone during ontogeny. In the compacta of long bones, the density of vascular canals is closely connected with the apposition rate of bone, i. e., a dense or sparse vascularization means a higher or lower growth rate, respectively (Chinsamy 1993; Steyer et al. 2004; Klein & Sander 2008, and references therein). The higher growth rate requires a dense vascularization since faster growing bone has higher energy demands. With increasing age of the animals, vascularization and growth rate of the long bone cortices decreased, and the diameter of the vascular spaces becomes increasingly smaller due to their infilling with bone (Klein & Sander 2008). Although these studies focused on growth rates in long bone compacta, a similar connection between vascularization and bone growth can also be assumed in dermal bones. The better vascularization of the more interior than the more external part of the external cortex in the dermal bones investigated here might suggest that the bone growth was faster in an earlier ontogenetic stage and slowed down later. It is not possible that the vascular canals developed after the formation of the bone, since primary canals are incorporated into the bone during its deposition (Francillon-Vieillot et al. 1990; Chinsamy-Turan 2005).

In this connection, it is interesting to regard the thin section of the clavicle of the small, juvenile *Mastodonsaurus*. The external cortex is penetrated by an anastomosing network of numerous primary osteons. In contrast to more advanced specimens of the same taxon, neither the density nor the diameter of the vascular spaces decrease towards the bone surface, and the organization of the vascular network is irregular compared to the succession of primary osteons parallel to the external surface in the older specimens. The presence of numerous primary osteons through-

Tab. 3. Summary of histological data concerning the internal cortices of the dermal bones investigated. For abbreviations, see text.

Taxon	Bone tissue	Vascularization	Extraneous fibers
Porolepiform and stem-tetrapods			
Laccognathus	isopedine	avascular	fine, perpendicular to bone surface
Panderichthys	isopedine	low	fine, perpendicular to bone surface
Acanthostega	PFB, isopedine	low	fine, perpendicular to bone surface
Greererpeton	isopedine	low	fine, perpendicular to bone surface
Temnospondyls			
Edops	coarse PFB	avascular	not visible
Eryops	coarse PFB > ISF	low	fine, oblique to bone surface
Acheloma	fine PFB	avascular	fine, oblique to bone surface
Sclerocephalus	?	low	?
Archegosaurus	coarse PFB	low	not visible
Kupferzellia	coarse PFB	low	not visible
Mastodonsaurus	coarse PFB > ISF	medium to low	fine, oblique to bone surface
Mastodonsaurus (juv.)	coarse PFB	high	not visible
Metoposaurus	fine PFB	avascular	not visible
Plagiosuchus	coarse PFB	high	fine, oblique to bone surface
Plagiosternum	coarse PFB	high (interior)	fine, oblique to bone surface
Gerrothorax	coarse PFB	low	coarse, oblique to bone surface
Seymouriamorpha			
Seymouria	fine PFB	high	not visible

out the external cortex of the small specimen suggests a rather rapid formation of the bone (Margerie et al. 2002). However, the bone matrix proper in this specimen consists of parallel-fibered bone that has an intermediate growth rate between the slow-growing lamellar and the fast-growing woven or fibrous bone (Francillon-Vieillot et al. 1990), so that the growth rate cannot be compared e. g. with that of fast growing archosaurs (see e. g. Chinsamy-Turan 2005). However, the parallel-fibered bone is rather poorly organized in this specimen, indicating a higher growth rate than in well ordered parallel-fibered bone.

In the thin sections investigated here, the vascularization pattern of the internal cortex is similar to the external one in that the more interior portion is mostly better vascularized by primary vascular canals and primary osteons, whereas the internal portion is poorly vascularized or avascular (Tab. 3). In the small *Mastodonsaurus* specimen, the complete internal cortex is well vascularized, corresponding to the external cortex.

The secondary bone in the external cortex of *Edops*, *Eryops*, *Pantylus* and *Mastodonsaurus* that formed possibly after trauma or infection (see above) is much better vascularized than the adjacent primary bone. This could be explained by the enhanced physiological need for blood supply during bone repair.

4.3. Bone texture and implications for the mode of life

The middle region of the investigated dermal bones exhibits varying degrees of vascularization, resorption and secondary bone growth (Tab. 4). *Laccognathus* and the stem-tetrapods investigated here have a cancellous middle region that may show large erosion spaces in some areas, with irregular and rather thick trabeculae. Secondary remodeling is present, but Haversian tissue is not formed. Crown-group tetrapods like *Edops*, *Chenoprosopus*, *Eryops*, *Metoposaurus*, *Gerrothorax*, *Kupferzellia* and *Mastodonsaurus* are heavily ossified, and the middle region possesses numerous secondary osteons (often forming Haversian tissue) and stout, thick trabeculae. In contrast, *Plagiosuchus* shows very little secondary remodeling in its dermal bones, and a clear diploë structure is not present since the rather compact middle region is populated mostly by small primary vascular canals and primary osteons, similar to the osteoderms of this plagiosaurid (Witzmann & Soler-Gijón 2008). All these crown-group tetrapods lived primarily aquatically and were probably not rapid and agile swimmers but rather ambush predators, and the weight of the skeleton would have helped them to dive and to stay under water. De Ricqlès & de Buffrénil (2001) found osteosclerosis in the ribs of *Mastodonsaurus* and pachyostosis in the ribs of *Gerrothorax*, which fits into this interpretation. Only the postcranial skeleton of *Eryops* has adaptions for larger land excursions (Pawley & Warren 2006), although this animal was certainly still feeding in water (Schoch 2009) where it was lurking for prey.

Archegosaurus has more lightly built dermal skull bones since the middle region is trabecular with large erosive spaces. This gharial-like temnospondyl is interpreted as an active swimmer searching for fishes in the

Tab. 4. Summary of histological data concerning the middle region of the dermal bones investigated. Abbreviation: trab., trabecular. For further abbreviations, see text.

Taxon	Primary tissue	Vascularization	Bone texture	Haversian tissue
Porolepiform and stem-tetrapods				
Laccognathus	fine PFB	high (PO and SO)	coarse cancellous (trab.)	absent
Panderichthys	fine PFB	high (PO and SO)	coarse cancellous	absent
Acanthostega	fine PFB	high (PO and SO)	coarse cancellous	absent
Greererpeton	fine PFB	high (PO and SO)	fine to coarse cancellous	absent
Temnospondyls				
Edops	PFB > ISF	high (SO and PO)	fine to coarse cancellous	present
Chenoprosopus	PFB > ISF	high (SO)	fine to coarse cancellous	present
Eryops	PFB > ISF	high (SO)	coarse cancellous (trab.)	present
Acheloma	fine PFB	high (SO and ER)	trabecular	absent
Sclerocephalus	?	high (SO and ER)	trabecular	absent
Archegosaurus	fine PFB	high (SO)	trabecular	absent
Kupferzellia	PFB > ISF	high (SO)	coarse cancellous	absent
Mastodonsaurus	PFB, ISF	high (SO and PO)	coarse cancellous (trab.)	present
Mastodonsaurus (juv.)	coarse PFB	high (SO and PO)	fine to coarse cancellous	absent
Metoposaurus	fine PFB	high (SO)	coarse cancellous	present
Plagiosuchus	ISF, PFB	high (PVC, PO, ER)	fine cancellous	absent
Plagiosternum	fine PFB	high (SO, ER)	trabecular	absent
Gerrothorax	PFB, ISF	high (PO, SO, ER)	coarse cancellous to trab.	present
Lepospondyls				
Diplocaulus	PFB, ISF	high (SO, ER)	trabecular	absent
Pantylus	fine PFB	high (SO, ER)	trabecular	absent
Seymouriamorpha				
Seymouria	fine PFB	moderate (SO, PO)	fine to coarse cancellous	absent
Eureptilia				
Labidosaurus	fine PFB	high (SO)	coarse cancellous	present

open water (Witzmann & Schoch 2006). The dermal bone of the subadult *Sclerocephalus* skull investigated here has a similar microstructure. At least the juvenile and subadult individuals of this taxon can be interpreted as rather agile predators, as indicated by their slender body outline, the long, deep swimming tail and the flexible gastral scales (Witzmann 2007; Schoch & Witzmann 2009).

The nectridean *Diplocaulus* shows a completely different microstructure of its dermal skull bones compared to the above mentioned temnospondyls. The cortices are much reduced and the extended middle region is composed of large erosive cavities that are framed by very thin, regularly arranged trabeculae. This highly porous structure is the result of extensive erosion and remodeling, and it can be designated as an 'osteoporotic-like condition' in the sense of de Ricqlès & de Buffrénil (2001). The histological data of the dermal skull of *Diplocaulus* and the implication of skeletal lightening is in accordance with the palaeobiological hypothesis concerning the mode of life of this animal by Cruickshank & Skews (1980). These authors showed on the basis of wind tunnel tests that the expanded posterolateral 'horns' of the flat, boomerang-shaped skull of *Diplocaulus* served as a hydrofoil that produced positive lift in slowly moving water of streams, that enabled this animal to rise rapidly of the substrate towards the prey in the water column. The reduced skeletal mass observed in the *Diplocaulus* skull certainly enhanced the agility of the animal as well as its capability to accelerate quickly. However, to gain a more integrated picture, it would be interesting to investigate also the postcranial elements of *Diplocaulus* (ribs, vertebrae, limb bones) concerning their microstructure in the future.

The new skull reconstruction of *Plagiosternum* by Gastou (2007) shows that this plagiosaurid has a skull shape that is strikingly similar to that of *Diplocaulus*, and a corresponding function as a hydrofoil is well possible. This is supported by the fact that the dermal bones of *Plagiosternum* investigated here are also lightly built with extensive erosion cavities in the middle region. Unfortunately, the postcranial anatomy of *Plagiosternum* is too poorly known to gain further information about its mode of life.

4.4. Implications of bone histology for the soft tissue dermis

4.4.1. Metaplastic bone

Metaplastic bone develops via direct transformation of pre-existing, dense connective tissue (Haines & Mohuiddin 1968). Since a periost and thus osteoblasts are absent

during metaplastic ossification (but not always, see SCHEYER et al. 2008), fibroblasts take over the role of osteoblastic cells (VICKARYOUS & HALL 2008). According to HAINES & MOHUIDDIN (1968), metaplastic bone is a dense fibrous tissue whose coarse fibers are interwoven, and the bone cell lacunae are arranged irregularly and have mostly short or stumpy canaliculi. In accordance, the interwoven structural fibers described here in the dermal bones of skull and pectoral girdle of basal tetrapods can be interpreted as metaplastic in origin. However, none of the dermal bones investigated are composed completely of interwoven structural fibers. Interwoven structural fibers are found often as islets or larger areas in the more interior part of the external cortex, whereas the more external part consists often of parallel-fibered bone. As pointed out by MAIN et al. (2005), there exist many intermediate states between the periosteal bone of 'normal intramebraneous bone' and the metaplastic bone, and transitions from metaplastic to periosteal tissue can be observed in the same section (e. g., interwoven structural fibers to parallel-fibered bone; see also GOODWIN & HORNER 2004, SCHEYER & SÁNCHEZ-VILLAGRA 2007 and WITZMANN & SOLER-GIJÓN 2008). Apart from the basal tetrapods described in this study, metaplastic tissue has been found within the periosteal bone in the skull of pachycephalosaur dinosaurs (GOODWIN & HORNER 2004), in the ornamentation of abelisaurid theropod skulls (HIERONYMUS & WITMER 2008), in dermal bones of the turtle shell (SCHEYER & SÁNCHEZ-VILLAGRA 2007) and in osteoderms of several tetrapod taxa such as chroniosuchians and temnospondyls (WITZMANN & SOLER-GIJÓN 2008), extant squamates (ZYLBERBERG & CASTANET 1985; LEVRAT-CALVIAC & ZYLBERBERG 1986), fossil and extant archosaurs (e. g., DE RICQLÈS et al. 2001; MAIN et al. 2005; SCHEYER & SANDER 2004; VICKARYOUS & HALL 2008), and extant anurans (RUIBAL & SHOEMAKER 1984). Whereas VICKARYOUS & HALL (2006) found no evidence of metaplasia in the dermal armour of the extant armadillo *Dasypus*, HILL (2006) demonstrated characteristics of metaplastic tissue in fossil and extant xenarthran osteoderms.

The prerequisite for metaplastic development of bone is a dense connective tissue, e. g. articulation facets, attachment sites of tendons and ligaments, or a dense dermis (HAINES & MOHUIDDIN 1968). Because metaplastic bone develops via direct transformation of preexisting connective tissue, its occurrence in dermal bones of several basal crown-group tetrapods investigated here might indicate that their dermis was rather dense and composed of an interwoven network of strong collagenous fiber bundles. A mechanical advantage of metaplastic bone is a firm connection between bone and overlying soft-tissue, since the collagen fibers of the attached soft tissue are confluent with the collagen fibers within the metaplastic bone (HAINES & MOHUIDDIN 1968).

4.4.2. Sharpey's fibers

The often closely packed, well-mineralized Sharpey's fibers are numerous especially in the ridges and tubercles, and support the assumption of a rather dense integument in most investigated basal tetrapods. Sharpey's fibers represent pre-existing fibers of the dermis that became progressively incorporated in the external cortex during its growth. A very similar pattern of Sharpey's fibers has been reported in the shell bones of many turtles, in which dense connective tissue is tightly anchored to the sculptural projections of the dermal bones (SCHEYER & ANQUETIN 2008). Also HILL (2006) described closely spaced, ossified Sharpey's fibers that extend perpendicular to the external bone surface of xenarthran osteoderms and interweave with the collagen-fibers of the overlying dermis. Similarly, extraneous fibers firmly connect the scales of many teleosts (SIRE 1985, 1986) or the osteoderms of squamates (ZYLBERBERG & CASTANET 1985; LEVRAT-CALVIAC & ZYLBERBERG 1986) with the overlying integument. In these forms, the anchoring fibers extend uninterrupted from the bone into the dermis and continue until to the basement membrane of the epidermal-dermal boundary.

In general, the mineralization of Sharpey's fibers themselves can vary considerably, and the degree of their mineralization is probably associated with their mechanical effectiveness (JONES & BOYDE 1974; SILVA & MERZEL 2004). The mineralized fibers in basal tetrapods, especially when they have attained a large diameter, suggest a tight anchorage of the dermis to the external bone surface, particularly to the sculptural ridges and tubercles, which served as the main points of anchorage for the skin.

4.5. Dermal bone histology and the fish-tetrapod transition

4.5.1. The bone structure

Dermal sculpture that consists of bony tubercles and ridges is no acquisition of basal tetrapods, but developed already in their finned stem-forms after the reduction of the dental components (odontodes) in the dermal bones (see below). The basic morphology of the dermal sculpture, its morphogenesis by preferential growth, and its association with Sharpey's fibers was retained during the fish-tetrapod transition and was basically conserved in the different lineages of basal tetrapods including basal amniotes. In this respect, the dermal bones of basal tetrapods are highly conservative, and this applies also to the diploë-structure with compact external and internal cortices framing a cancellous to trabecular middle region that is affected by secondary remodeling to varying degrees.

The dermal bones of the limbed stem-tetrapods *Acan-*

thostega and *Greererpeton* are more 'fish-like' compared to those of the crown-group tetrapods in the possession of isopedine in the internal cortex, a tissue that has so far not been demonstrated in limbed tetrapods, and in the thinner Sharpey's fibers within the external cortex. Similar to the finned sarcopterygians, the primary bone matrix of external cortex and middle region is mainly composed of parallel-fibered bone. However, limbed stem-tetrapods are more 'tetrapod-like' in that the bony tubercles and ridges (the 'pit and ridge-sculpture') are more pronounced and form a stronger relief.

In crown-group tetrapods, the sculpture is generally even more pronounced, what surely led to an increased consolidation of the bone-dermis contact, and also the Sharpey's fiber morphology shows differences. In the porolepiform *Laccognathus*, the Sharpey's fibers that penetrated the bone surface between the odontodes were unmineralized, whereas the fibers are well mineralized in the basal tetrapods investigated here. Interestingly, the Sharpey's fibers are distinctly larger in diameter in most basal crown-group tetrapods than in *Laccognathus* and stem-tetrapods (Tab. 2), and often more densely arranged. Compared to the finned sarcopterygians and stem-tetrapods, the degree of remodeling and the number and density of secondary osteons are generally higher, with the exception of *Plagiosuchus*, in which secondary osteons are very scarce and thus gives a 'juvenile' impression. Furthermore, the cancellous to trabecular middle region occupies a proportionally larger space in most investigated basal crown-group tetrapods with respect to the compact cortices. The primary bone matrix in basal crown-group tetrapods consists to a large degree of parallel-fibered bone, and this holds true also for the internal cortex, where isopedine is completely reduced. However, also primary interwoven structural fibers can be recognized in the dermal bones, in contrast to *Laccognathus* and stem-tetrapods. The ability of the tetrapod dermis to form this metaplastic tissue might have evolved somewhere before the split into the amphibian- (temnospondyl-) and amniote lineage in a stem-tetrapod more crownwards than *Greererpeton*. This is in accordance with the study of Sire & Huysseune (2003), who found a 'normal' periosteal development without evidence of metaplasia in the postcranial armour plates of extant fishes.

4.5.2. The soft-tissue integument

If the interpretations based on the occurrence of metaplastic tissue and Sharpey's fiber morphology outlined in chapter 4.4. are correct, then many basal crown-group tetrapods had a more consolidated integument compared to *Laccognathus* and the stem-tetrapods investigated, that might be associated with their different modes of life. Like finned sarcopterygians, *Acanthostega* and *Greererpeton* probably possessed internal gills (Clack 2000; Lebedev & Coates 1995). They were primarily water dwellers that were nevertheless probably able to crawl on the shore, but not to walk effectively on land (Carroll et al. 2005). In contrast, the earliest known temnospondyls of the Carboniferous are suggested to be capable of larger land excursions (Milner & Sequeira 1994; Holmes et al. 1998). Therefore, a denser integument might have been required to reduce the extent of water loss in air and to withstand mechanical friction and abrasion during locomotion on land. The fact that the number and density of Sharpey's fibers are generally reduced in the external cortex of *Mastodonsaurus* could be explained with the larger amount of interwoven structural fibers in the external cortex of this taxon. As outlined by Haines & Mohuiddin (1968), soft tissue is tightly anchored to metaplastic bone because the collagen fibers course uninterrupted between bone and soft-tissue. This can also be assumed for external cortex and overlying dermis of these capitosauroids, rendering a larger number of Sharpey's fibers unnecessary. In contrast, *Metoposaurus* has an external cortex that is solely composed of well-ordered parallel-fibered bone with no metaplastic tissue, and numerous clusters of densely arranged Sharpey's fibers connected the integument to the bone surface.

4.6. Odontodes and bony sculpture

4.6.1. Spatial arrangement of odontodes and bony ridges and tubercles

The presence of dental tissue (dentine and enamel/enameloid) on the external surface of dermal bones as either tubercles or ridges (odontodes; see description of *Laccognathus* above) can be regarded as plesiomorphic for osteichthyans and even for vertebrates in general (e. g., Ørvig 1968, 1977; Reif 1982; Smith & Hall 1993; Janvier 1996). These dental components of the exoskeleton were reduced during the evolution of distinct vertebrate lineages, and also independently within actinopterygians and different groups of finned sarcopterygians. Also in tetrapods and their immediate stem-forms from tristichopterids (including *Eusthenopteron*) crownwards, all non-oral dental elements were lost, and the tubercles and ridges on the dermal bone surface consist completely of bone (Bystrow 1939; Gross 1957; Ørvig 1977; Reif 1982; Janvier 1996).

In thin sections of odontode-bearing dermal bones of several 'ostracoderms', arthrodires, actinopterygians and finned sarcopterygians, different generations of odontodes are frequently visible within the external cortex, with the older generations being buried within the growing bone matrix (e. g., Pander 1860; Gross 1930; Bystrow 1939;

ØRVIG 1977; SMITH 1977) (see also Fig. 2c). A very similar pattern of superpositional growth is shown by the sculptural tubercles or ridges that consist completely of bone, e. g. in the basal tetrapods and their stem-forms investigated here (Figs. 2e, 11d). 'Buried' bony tubercles of earlier generations are generally readily visible in the bone matrix of the external cortex, closely resembling the spatial arrangement of successive generations of odontodes. A further similarity is that the odontodes/bony tubercles of successive generations are generally larger than those of preceding generations (e. g., BYSTROW 1935, 1939; ØRVIG 1977; this study). This similarity in arrangement, spatial distribution and outer morphology of the bony sculpture and the odontodes suggests that the bony tubercles and ridges have taken over parts of the functional role of the odontodes. This is supported by the histology of the dermal tubercles e. g. in the Devonian fish-like sarcopterygian *Holoptychius*. BYSTROW (1939, fig. 10a, b) investigated thin sections of dermal skull bones of this porolepiform and found the sculptural tubercles to be composed of both bone and dentine, and noted the absence of enamel. He interpreted this as an evolutionary 'transformation' (Verwandlung) of dermal teeth (odontodes) into bony tubercles within 'crossopterygians' (BYSTROW 1939: 303; see also ØRVIG 1977).

4.6.2. Functional considerations and the reduction of odontodes

The dentinous tissue of the odontodes was formed during ontogeny in a dental papilla (consisting of mesenchymal soft tissue) in the dermis directly below the epidermal-dermal junction, and enamel was produced by the adjoining dental organ (consisting of epidermis cells) in the basal part of the epidermis (ØRVIG 1977; REIF 1982). In contrast to odontodes, which arose always in the superficial part of the dermis, the supporting, comparatively thick dermal bone developed in the middle and internal parts of the dermis (ØRVIG 1968). By the interactions of epidermal and ectomesenchymal tissue in the production of the odontodes, and their development above (enamel) and below (dentine and bone) the epidermal-dermal junction, the outer skeletal surface might have been well integrated with both dermis and epidermis via the odontodes. Furthermore, because of the superficial position of the odontodes within the skin (the enamel cap might have extended beyond the soft-tissue integument, or it was covered solely by epidermis cells; see ØRVIG 1977, fig. 1), they stabilized the integument and served for mechanical protection (e. g. against abrasion) of the soft-tissue including the vessels and nerves that arose from the bone surface in the 'valleys' between the odontodes.

The epidermal (and superficial dermal) portion of the exoskeleton was lost when the odontodes were reduced and replaced by bony tubercles and ridges. As indicated by the occurrence of the mostly densely arranged Sharpey's fibers, these bony sculptural elements laid deeper in the integument than the odontodes and were covered by the dermis, and there are no indications that they extended until to the epidermis. REM studies reveal no imprints of epithelial cells as visible e. g. in the cosmine covering of dermal bones in fossil lungfishes (SMITH 1977; BEMIS & NORTHCUTT 1992). Analogous to certain fishes and squamates (see above), it is hypothesized here that the bundles of Sharpey's fibers, that are found mainly and most closely packed in the bony tubercles and ridges, still maintained an association between the outer surface of the dermal bone and the superficial parts of the dermis and epidermal-dermal junction, respectively. These extrinsic fibers led to a strengthening of the integument and its tight connection to the bone surface. Like the odontodes, the bony ridges and tubercles certainly also protected the numerous blood vessels mechanically that coursed in furrows or pits between them. The difference, however, is that the bony tubercles and ridges were embedded deeper within the dermis and did not extend to or beyond the epidermis (see above). This might be the reason why the skin became more dense and was more tightly bound to the bone surface by Sharpey's fibers after the odontodes were reduced; this difference is well visible between the odontode-bearing *Laccognathus* with loosely arranged, unmineralized Sharpey's fibers (Fig. 2a, c) and *Panderichthys*, that has a bony sculpture and stronger, mineralized extrinsic fibers (Fig. 2e).

5. Conclusions

The thick, well mineralized Sharpey's fibers and the presence of metaplastic tissue suggest that the first crown-group tetrapods had attained a denser integument than their stem-forms. The more consolidated integument probably provided a better resistance against water loss and mechanical damage such as abrasion during locomotion on land. Additional to this, there is also evidence that the epidermis in basal tetrapods was more similar to amniotes in being more strongly cornified and more complex compared to lissamphibians (MADDIN et al. 2007). These implications for the soft-tissue integument, the presence of well-ossified scales in the majority of Palaeozoic basal tetrapods (WITZMANN 2007) and the often large size of these animals strongly suggest that cutaneous respiration was not as substantial as in extant slamanders and anurans. It might have been comparably important in small-growing, newt-like forms like branchiosaurids (BOY 1993) or the miniaturized lepospondyls (SCHOCH & CARROLL 2003). The thin, moist integument of extant amphibians, which is suitable to large-scale cutaneous gas exchange, can there-

fore probably be regarded as derived and is an adaptation to their small size, as already suggested by ROMER (1972). The 'rete vasculosum' did not serve for the purpose of cutaneous respiration as proposed by BYSTROW (1947), but rather for supply of the dermal bone during its growth.

6. References

BEMIS, W. E. & NORTHCUTT, R. G. (1992): Skin and blood vessels of the snout of the Australian Lungfish, *Neoceratodus forsteri*, and their significance for interpreting the cosmine of Devonian lungfishes. Acta Zoologica (Stockholm), **73**: 115 139.

BOY, J. A. (1993): Synopsis of the tetrapods from the Rotliegend (Lower Permian) in the Saar-Nahe Basin (SW-Germany). In: HEIDTKE, U. (ed.): New Research on Permo-Carboniferous Faunas. Pollichia-Buch, **29**: 155 169.

BOYDE, A. (1972): Scanning electron microscopic studies of bone. In: BOURNE, G. (ed.): The biochemistry and physiology of bone, Vol. 1: 259 309; New York (Academic Press).

BUFFRÉNIL, V. DE (1982): Morphogenesis of bone ornamentation in extant and extinct crocodilians. Zoomorphologie, **99**: 155 166.

BUFFRÉNIL, V. DE, FARLOW, J. O. & RICQLÈS, A. DE. (1986): Growth and function of *Stegosaurus* plates: evidence from bone histology. Paleobiology, **12**: 459 473.

BYSTROW, A. P. (1935): Morphologische Untersuchungen der Deckknochen des Schädels der Stegocephalen. 1. Mitteilung. Schädel der Stegocephalen. Acta Zoologica (Stockholm), **16**: 65 141.

BYSTROW, A. P. (1939): Zahnstruktur der Crossopterygier. Acta Zoologica (Stockholm), **20**: 283 338.

BYSTROW, A. P. (1942): Deckknochen und Zähne der *Osteolepis* und *Dipterus*. Acta Zoologica (Stockholm), **23**: 263 289.

BYSTROW, A. P. (1947): Hydrophilous and xerophilous labyrinthodonts. Acta Zoologica (Stockholm), **28**: 137 164.

BYSTROW, A. P. (1957): The microstructure of dermal bones in arthrodires. Acta Zoologica (Stockholm), **38**: 239 275.

CARROLL, R. L., IRWIN, J. & GREEN, D. M. (2005): Thermal physiology and the origin of terrestriality in vertebrates. Zoological Journal of the Linnean Society, **143**: 345 358.

CASTANET, J., FRANCILLON-VIEILLOT, H., RICQLÈS, A. DE & ZYLBERBERG, L. (2003): The skeletal histology of the Amphibia. In: HEATWOLE, H. & DAVIES, M. (eds.): Amphibian Biology, Vol. **5**: Osteology: 1598 1683; Chipping Norton (Surrey Beatty).

CHINSAMY, A. (1993): Image analysis and the physiological implications of the vascularisation of femora in archosaurs. Modern Geology, **19**: 101 108.

CHINSAMY, A. & RAATH, M. A. (1992): Preparation of fossil bone for histological examination. Palaeontographica africana, **29**: 39 44.

CHINSAMY-TURAN, A. (2005): The microstructure of dinosaur bone. Deciphering biology with fine-scale techniques. 195 pp.; Baltimore (Johns Hopkins University Press).

CLACK, J. A. (2000): The origin of tetrapods. In: HEATWOLE, H. & CARROLL, R. L. (eds.): Amphibian Biology, Vol. **4**: Palaeontology: 979 1029; Chipping Norton (Surrey Beatty).

CLOUTIER, R. & AHLBERG, P. E. (1996): Morphology, characters, and the interrelationships of basal sarcopterygians. In: STIASSNY, M. L. J., PARENTI, L. R. & JOHNSON, G. D. (eds.): Interrelationships of fishes: 445 480; San Diego (Academic Press).

COLDIRON, R. W. (1974): Possible functions of ornament in labyrinthodont amphibians. Occasional Papers of the Museum of Natural History, University of Kansas, **33**: 1 19.

COSGRIFF, J. W. & ZAWISKIE, J. M. (1979): A new species of the Rhytidosteidae from the *Lystrosaurus* zone and a review of the Rhytidosteoidea. Palaeontologica africana, **22**: 1 27.

CREDNER, H. (1893): Die Stegocephalen aus dem Rotliegenden des Plauen'schen Grundes bei Dresden. 10. Theil. Zeitschrift der Deutschen Geologischen Gesellschaft, **45**: 639 704.

CRUICKSHANK, A. R. I. & SKEWS, B. W. (1980): The functional significance of nectridean tabular horns (Amphibia: Lepospondyli). Proceedings of the Royal Society of London, Series B, **209**: 513 537.

DAMIANI, R. J. (2000): Bone histology of some Australian Triassic temnospondyl amphibians: preliminary data. Modern Geology, **24**: 109 124.

ENLOW, D. H. & BROWN, S. O. (1956): A comparative histological study of fossil and recent bone tissues. Part I. Texas Journal of Science, **8**: 405 443.

FRANCILLON-VIEILLOT, H., BUFFRÉNIL, V. DE, CASTANET, J., GERAUDIE, J., MEUNIER, F. J., SIRE J.-Y., ZYLBERBERG, L. & RICQLÈS, A. DE (1990): Microstructure and mineralization of vertebrate skeletal tissues. In: CARTER, J. G. (ed.): Biomineralization: Patterns and Evolutionary Trends: 471 530; New York (Van Nostrand Reinhold).

GASTOU, S. (2007): A revision of the plagiosaurid *Plagiosternum granulosum* FRAAS (Amphibia: Temnospondyli) from the Middle Triassic of Germany. Unpublished DES Report, Université Paris 6.

GOODWIN, M. B. & HORNER, J. R. (2004): Cranial histology of pachycephalosaurs (Ornithischia: Marginocephalia) reveals transitory structures inconsistent with head-butting behavior. Paleobiology, **30**: 252 267.

GROSS, W. (1930): Die Fische des mittleren Old Red Süd-Livlands. Geologische und Paläontologische Abhandlungen, **22**: 123 156.

GROSS, W. (1934): Die Typen des mikroskopischen Knochenbaues bei fossilen Stegocephalen und Reptilien. Zeitschrift für Anatomie und Entwicklungsgeschichte, **103**: 731 764.

GROSS, W. (1957): Mundzähne und Hautzähne der Acanthodier und Arthrodiren. Palaeontographica, Abteilung A, **109**: 1 40.

GROSS, W. (1973): Kleinschuppen, Flossenstacheln und Zähne von Fischen aus europäischen und nordamerikanischen bonebeds des Devons. Palaeontographica, Abteilung A, **142**: 51 155.

HAINES, R. W. & MOHUIDDIN, A. (1968): Metaplastic bone. Journal of Anatomy, **103**: 527 538.

HENNIG, W. (1966): Phylogenetic Systematics. 280 pp.; Champaign (University of Illinois Press).

HIERONYMUS, T. & WITMER, L. (2008): The facial skin of *Majungasaurus crenatissimus* (Abelisauridae: Saurischia): pronounced dermal metaplasia as the cause of rugosity in abelisaurid skulls. Journal of Vertebrate Paleontology, **28** (Supplement): 90A.

HILL, R. V. (2005): Integration of morphological data sets for phylogenetic analysis of Amniota: the importance of integumentary characters and increased taxonomic sampling. Systematic Biology, **54**: 1 18.

HILL, R. V. (2006): Comparative anatomy and histology of xenarthran osteoderms. Journal of Morphology, **267**: 1441 1460.

HOLMES, R. R., CARROLL, R. L. & REISZ, R. R. (1998): The first articulated skeleton of *Dendrerpeton acadianum* (Temnospondyli, Dendrerpetontidae) from the Lower Pennsylvanian locality in Joggins, Nova Scotia, and a review of its re-

lationships. Journal of Vertebrate Paleontology, **18**: 64 79.

Janvier, P. (1996): Early Vertebrates. Reprint 2002. 393 pp.; Oxford (Clarendon Press).

Jones, S. J. & Boyde, A. (1974): The organization and gross mineralization patterns of the collagen fibers in Sharpey fiber bone. Cell Tissue Research, **148**: 83 96.

Kissel, R. A., Dilkes, D. W. & Reisz, R. R. (2002): *Captorhinus magnus*, a new captorhinid (Amniota: Eureptilia) from the Lower Permian of Oklahoma, with new evidence on the homology of the astragalus. Canadian Journal of Earth Sciences, **39**: 1363 1372.

Klein, N. & Sander, P. M. (2007): Bone histology and growth of the prosauropod dinosaur *Plateosaurus engelhardti* von Meyer, 1837 from the Norian bonebeds of Trossingen (Germany) and Frick (Switzerland). Special Papers in Palaeontology, **77**: 169 206.

Klein, N. & Sander, P. M. (2008): Ontogenetic stages in the long bone histology of sauropod dinosaurs. Paleobiology, **34**: 247 263.

Lebedev, O. A. & Coates, M. I. (1995): The postcranial skeleton of the Devonian tetrapod *Tulerpeton curtum* Lebedev. Zoological Journal of the Linnean Society, **114**: 307 348.

Levrat-Calviac, V. & Zylberberg, L. (1986): The structure of the osteoderms in the gekko: *Tarentola mauritanica*. American Journal of Anatomy, **176**: 437 446.

Maddin, H. C., Musat-Marcu, S. & Reisz, R. R. (2007): Histological microstructure of the claws of the African Clawed Frog, *Xenopus laevis* (Anura: Pipidae): implications for the evolution of claws in tetrapods. Journal of Experimental Zoology, Part B, Molecular and Developmental Evolution, **308**: 259 268.

Main, R. P., Ricqlès, A. de, Horner, J. R. & Padian, K. (2005): The evolution and function of thyreophoran dinosaur scutes: implications for plate function in stegosaurs. Paleobiology, **31**: 291 314.

Margerie, E. de, Cubo, J. & Castanet, J. (2002): Bone typology and growth rate: testing and quantifying 'Amprino's rule' in the mallard (*Anas platyrhynchos*). Comptes rendus biologies, **325**: 221 230.

Milner, A. R. & Sequeira, S. E. K. (1994): The temnospondyl amphibians from the Viséan of East Kirkton, West Lothian, Scotland. Transactions of the Royal Society of Edinburgh, Earth Sciences, **84**: 331 361.

Modesto, S., Scott, D. M., Berman, D. S., Müller, J. & Reisz, R. (2007): The skull and the palaeoecological significance of *Labidosaurus hamatus*, a captorhinid reptile from the Lower Permian of Texas. Zoological Journal of the Linnean Society, **149**: 237 262.

Mowbray, K. (2005): Surface bone histology of the occipital bone in humans and chimpanzees. The Anatomical Record, Part B, **283**: 14 22.

Ørvig, T. (1951): Histologic studies of placoderms and fossil elasmobranchs. 1. The endoskeleton, with remarks on the hard tissues of lower vertebrates in general. Arkiv för Zoologi, **2**: 321 453.

Ørvig, T. (1957): Remarks on the vertebrate fauna of the Lower Devonian of Escuminac Bay, P.Q., Canada, with special reference to the porolepiform crossopterygians. Arkiv för Zoologi, **10**: 367 426.

Ørvig, T. (1966): Histologic studies of ostracoderms, placoderms and fossil elasmobranchs. 2. On the dermal skeleton of two late Palaeozoic elasmobranchs. Arkiv för Zoologi, **19**: 1 39.

Ørvig, T. (1968): The dermal skeleton; general considerations. In: Ørvig, T. (ed.): Current problems of lower vertebrate phylogeny, Proceedings of the 4th Nobel Symposium: 373 397; Stockholm (Almquist & Wiksell).

Ørvig, T. (1977): A survey of odontodes ('dermal teeth') from developmental, structural, functional, and phyletic points of view. In: Andrews, S. M., Miles, R. S. & Walker, A. D. (eds.): Problems in vertebrate evolution. Linnean Society Symposium Series, **4**: 53 75.

Ørvig, T. (1989): Histologic studies of ostracoderms, placoderms and fossil elasmobranchs. 6. Hard tissues of Ordovician vertebrates. Zoologica Scripta, **18**: 427 446.

Pander, C. H. (1860): Über die Saurodipterinen, Dendrodonten, Glyptolepiden und Cheirolepiden des devonischen Systems. 96 pp.; Petersburg (Kaiserliche Akademie der Wissenschaften).

Pawley, K. & Warren, A. A. (2006): The appendicular skeleton of *Eryops megacephalus* Cope, 1877 (Temnospondyli: Eryopoidea) from the Lower Permian of North America. Journal of Paleontology, **80**: 561 580.

Peabody, F. (1961): Annual growth zones in living and fossil vertebrates. Journal of Morphology, **108**: 11 62.

Reif, W.-E. (1982): Evolution of dermal skeleton and dentition in vertebrates the odontode regulation theory. Evolutionary Biology, **15**: 287 368.

Ricqlès, A. de (1975a): Quelques remarques paléohistologiques sur le problème de la néoténie chez les Stégocéphales. Problèmes Actuels de Paléontologie: Evolution des Vertébrés. Colloque International du Centre National de Recherche Scientifique, **218**: 351 363.

Ricqlès, A. de (1975b): Recherches paléohistologiques sur les os longs des tétrapodes. VII. Sur la classification, la signification fonctionnelle et l'histoire des tissus osseux des tétrapodes. Première partie. Annales de Paléontologie (Vertébrés), **61**: 51 129.

Ricqlès, A. de (1976): Recherches paléohistologiques sur les os longs des tétrapodes. VII. Sur la classification, la signification fonctionnelle et l'histoire des tissus osseux des tétrapodes. Deuxième partie. Annales de Paléontologie (Vertébrés), **62**: 71 126.

Ricqlès, A. de (1977): Recherches paléohistologiques sur les os longs des tétrapodes. VII. Sur la classification, la signification fonctionnelle et l'histoire des tissus osseux des tétrapodes. Deuxième partie, suite. Annales de Paléontologie (Vertébrés), **63**: 33 56.

Ricqlès, A. de (1981): Recherches paléohistologiques sur les os longs des tétrapodes. VI. Stégocéphales. Annales de Paléontologie (Vertébrés), **67**: 141 160.

Ricqlès, A. de (1993): Some remarks on palaeohistology from a comparative evolutionary point of view. In: Grupe, G. & Garland, A. N. (eds.): Histology of ancient human bone: 37 77; Berlin (Springer).

Ricqlès, A. de & Buffrénil, V. de (2001): Bone histology, heterochronies and the return of tetrapods to life in water: where are we? In: Mazin, J.-M. & Buffrénil, V. de (eds.): Secondary adaptation of tetrapods to life in water: 289 310; Munich (Dr. Friedrich Pfeil).

Ricqlès, A. de, Meunier, F. J., Castanet, J. & Francillon-Vieillot, H. (1991): Comparative microstructure of bone. In: Hall, B. K. (ed.): Bone. Volume 3: Bone matrix and bone specific products: 1 78; Boca Raton (CRC Press).

Ricqlès, A. de, Pereda Superbiola, X., Gasparini, Z. & Olivero, E. (2001): Histology of dermal ossifications in an ankylosaurian dinosaur from the Late Cretaceous of Antarctica. Asociación Paleontológica Argentina, Publicación Especial, **7**: 171 174.

Romer, A. S. (1972): Skin breathing primary or secondary? Respiration Physiology, **14**: 183 192.

Ruibal, R. & Shoemaker, V. (1984): Osteoderms in anurans. Journal of Herpetology, **18**: 313 328.

Ruta, M., Coates, M. I. & Quicke, D. L. J. (2003): Early tetrapod relationships revisited. Biological Reviews, **78**: 251 345.

Sanchez, S., Klembara, J., Castanet, J. & Steyer, J. S. (2008): Salamander-like development in a seymouriamorph revealed by palaeohistology. Biology Letters, **4**: 411 414.

Sander, P. M. & Andrássy, P. (2006): Lines of arrested growth and long bone histology in Pleistocene large mammals from Germany: What do they tell us about dinosaur physiology? Palaeontographica, Abteilung A, **277**: 143 159.

Scheyer, T. M. (2007): Skeletal histology of the armor of the Placodontia: the occurrence of 'postcranial fibro-cartilaginous bone' and its developmental implications. Journal of Anatomy, **211**: 737 753.

Scheyer, T. M. & Anquetin, J. (2008): Bone histology of the Middle Jurassic turtle shell remains from Kirtlington, Oxfordshire, England. Lethaia, **41**: 85 96.

Scheyer, T. M. & Sánchez-Villagra, M. R. (2007): Carapace bone histology in the giant pleurodiran turtle *Stupendemys geographicus*: phylogeny and function. Acta Palaeontologica Polonica, **52**: 137 154.

Scheyer, T. M. & Sander, P. M. (2004): Histology of ankylosaur osteoderms: implications for systematics and function. Journal of Vertebrate Paleontology, **24**: 874 893.

Scheyer, T. M., Brüllmann, B. & Sánchez-Villagra, M. R. (2008): The ontogeny of the shell in side-necked turtles, with emphasis on the homologies of costal and neural bones. Journal of Morphology, **269**: 1008 1021.

Schoch, R. R. (2009): The evolution of life cycles in early amphibians. Annual Reviews of Earth and Planetary Sciences, **37**: 135 162.

Schoch, R. R. & Carroll, R. L. (2003): Ontogenetic evidence for the Paleozoic ancestry of salamanders. Evolution and Development, **5**: 314 324.

Schoch, R. R. & Witzmann, F. (2009): Osteology and relationships of the temnospondyl *Sclerocephalus*. – Zoological Journal of the Linnean Society, **157**: 135 168.

Seitz, L. (1907): Vergleichende Studien über den mikroskopischen Knochenbau fossiler und rezenter Reptilien. Nova acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum, **87**: 230 370.

Silva, M. A. J. & Merzel, J. (2004): Alveolar bone Sharpey fibers of the rat incisor in normal and altered functional conditions examined by scanning electron microscopy. The Anatomical Record, Part A, **279**: 792 797.

Sire, J.-Y. (1985): Fibers d'ancrage et couche limitante externe à la surface des écailles du Cichlidae *Hemichromis bimaculatus* (Téléostéen, Perciforme): données ultrastructurales. Annales des Sciences Naturelles, Zoologie, 13e série, **7**: 163 180.

Sire, J.-Y. (1986): Ontogenic development of surface ornamentation in the scales of *Hemichromis bimaculatus* (Cichlidae). Journal of Fish Biology, **28**: 713 724.

Sire, J.-Y. & Huysseune, A. (2003): Formation of dermal skeletal and dental tissues in fish: a comparative and evolutionary approach. Biological Reviews, **78**: 219 249.

Smith, M. M. (1977): The microstructure of the dentition and dermal ornament of three dipnoans from the Devonian of Western Australia: a contribution towards dipnoan interrelations, and morphogenesis, growth and adaptation of the skeletal tissues. Philosophical Transactions of the Royal Society of London, Series B, **281**: 29 72.

Smith, M. M. & Hall, B. K. (1993): A developmental model for evolution of the vertebrate exoskeleton and teeth: the role of cranial and trunk neural crest. Evolutionary Biology, **27**: 387 448.

Steyer, J. S., Laurin, M., Castanet, J. & Ricqlès, A. de (2004): First histological and skeletochronological data on temnospondyl growth: palaeoecological and palaeoclimatological implications. Palaeogeography, Palaeoclimatology, Palaeoecology, **206**: 193 201.

Thomson, K. S. (1977): On the individual history of cosmine and possible electroreceptive function of the pore canal system in fossil fishes. In: Andrews, S. M., Miles, R. S. & Walker, A. D. (eds.): Problems in vertebrate evolution: 247 270; London (Academic Press).

Vickaryous, M. K. & Hall, B. K. (2006): Osteoderm morphology and development in the Nine-Banded Armadillo, *Dasyceps novemcinctus* (Mammalia, Xenarthra, Cingulata). Journal of Morphology, **267**: 1273 1283.

Vickaryous, M. K. & Hall, B. K. (2008): Development of the dermal skeleton in *Alligator mississippiensis* (Archosauria, Crocodylia) with comments on the homology of osteoderms. Journal of Morphology, **269**: 398 422.

Witzmann, F. (2007): The evolution of the scalation pattern in temnospondyl amphibians. Zoological Journal of the Linnean Society, **150**: 815 834.

Witzmann, F. & Schoch, R. R. (2006): Skeletal development of the temnospondyl *Acanthostomatops vorax* from the Lower Permian Döhlen Basin of Saxony. Transactions of the Royal Society of Edinburgh: Earth Sciences, **96**: 365 385.

Witzmann, F. & Soler-Gijón, R. (2008): The bone histology of osteoderms in temnospondyl amphibians and in the chroniosuchian *Bystrowiella*. Acta Zoologica (Stockholm). DOI 10.1111/j.1463-6395.2008.00385.x

Yates, A. M. & Warren, A. A. (2000): The phylogeny of the 'higher' temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. Zoological Journal of the Linnean Society, **128**: 77 121.

Zhu, M. & Schultze, H.-P. (2001): Interrelationship of basal osteichthyans. In: Ahlberg, P. (ed.): Major events in vertebrate evolution: 289 314; London (Taylor & Francis).

Zylberberg, L. & Castanet, J. (1985): New data on the structure and the growth of the osteoderms in the reptile *Anguis fragilis* L. (Anguidae, Squamata). Journal of Morphology, **186**: 327 342.

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Dermal bone sculpture in early tetrapods: external morphology, histology and possible functions

Appendix 3

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Dermal bone in early tetrapods: a palaeophysiological hypothesis of adaptation for terrestrial acidosis

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The dermal bone sculpture of early, basal tetrapods of the Permo-Carboniferous is unlike the bone surface of any living vertebrate, and its function has long been obscure. Drawing from physiological studies of extant tetrapods, where dermal bone or other calcified tissues aid in regulating acid–base balance relating to hypercapnia (excess blood carbon dioxide) and/or lactate acidosis, we propose a similar function for these sculptured dermal bones in early tetrapods. Unlike the condition in modern reptiles, which experience hypercapnia when submerged in water, these animals would have experienced hypercapnia on land, owing to likely inefficient means of eliminating carbon dioxide. The different patterns of dermal bone sculpture in these tetrapods largely correlates with levels of terrestriality: sculpture is reduced or lost in stem amniotes that likely had the more efficient lung ventilation mode of costal aspiration, and in small-sized stem amphibians that would have been able to use the skin for gas exchange.

Keywords: early tetrapods; basal tetrapods; dermal bone; acidosis; hypercapnia

1. INTRODUCTION

The first tetrapods of the Late Devonian (385–365 Ma) were semi-aquatic forms, possessing lungs inherited from their fish ancestors [1]. The transition to life on land would have imposed several new physical constraints, including the absence of water's buoyancy to counteract gravity, the risk of dehydration and the need to perform all respiratory gas exchange via the lungs or skin.

The emergence of tetrapods has been related to low atmospheric oxygen levels in the later Palaeozoic (14–16% O_2 [2]), which would have severely limited oxygen availability in water owing to its low solubility [1]. Lungs would have been advantageous under these conditions, even for an aquatic animal gulping air; even relatively hypoxic air has many times more oxygen than a similar volume of normoxic water. However, the respiratory physiology of extant vertebrates strongly suggests that a terrestrial lifestyle would have been disadvantageous for these early tetrapods (both stem forms basal to the extant tetrapod lineages, and early members of the stem amniote and amphibian lineages) with regard to excretion of CO_2, even though Late Devonian and Early Carboniferous CO_2 levels were relatively low (0.3–0.35% [2]). Possible solutions to CO_2 excretion in early tetrapods have been extensively debated [3–8]: here we propose a novel mechanism by which these tetrapods might have tolerated CO_2 accumulation on land, relating to their integumental structure.

The integument of early tetrapods differed from that of earlier tetrapodomorph fish and of extant tetrapods, by the dermal bones of skull and pectoral girdle that were often highly sculptured (or ornamented) and/or thickened; there is as yet no entirely satisfactory explanation for this morphology [9–12].

Physiological studies on extant tetrapods lead us to the hypothesis that mineralized tissues, particularly sculptured dermal bones, may have functioned to buffer CO_2 and metabolic acids that would have accumulated in these early tetrapods during prolonged excursions onto land. We detail below the physiological problems entailed in CO_2 loss on land. Additionally, we note that terrestrial tetrapods would face greater exertion (and hence greater generation of metabolic CO_2) during locomotion on land than in the water, due to the higher costs of terrestrial locomotion [13].

This paper is speculative in its approach: at present it is impossible to confirm or refute our hypothesis with histological studies of fossil vertebrates, although future work on extant vertebrates may yield anatomical or chemical signatures that can be applied to fossils. Meanwhile, we demonstrate here that our hypothesis is strongly supported by the observed dermal morphology in the diversity of early tetrapods in correspondence with their presumed ecologies (terrestrial or aquatic), as determined by other anatomical features.

2. THE VERTEBRATE INTEGUMENT

Early tetrapods possessed various types of dermal mineralized elements [6,14–18]. The heavy dermal cover of some of these tetrapods, bearing a sculptured surface of pits and ridges, may be considered to be osteoderms, similar to those seen today in some reptiles and frogs [19]; but these can be distinguished from thinner,

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overlapping dermal scales in pockets of the dermis [20] that are an ancestral tetrapod feature [16,17,21]. Dermal bone does not block interaction between the dermis and the superficial integument because blood vessels run through it to the epidermis [22].

Many early tetrapods possessed dermal bones of the skull and pectoral girdle with an external (superficial) surface heavily sculptured by pits, ridges and furrows. The microanatomy of these dermal bones shows that they were extensively vascularized, with blood vessels opening to the bone surface within the sculptural pits and furrows [9,12]. The osteoderms of many early tetrapods have basically the same structure [18]. This extensive dermal cover is often referred to as 'dermal armour'.

Various hypotheses exist for the presence of sculptured dermal bones in early tetrapods: cutaneous respiration [9,10,23], strengthening adaptation [24], protection from desiccation [25], mechanical protection of the soft-tissue dermis including vessels and nerves [11,12] and thermoregulation [12,26]. The fact that this dermal sculpture is always associated with a high degree of vascularization indicates that this morphological feature certainly had a physiological significance. In contrast to sculptured bones, the smooth or weakly sculptured dermal bones of other early tetrapods are normally less vascularized in the superficial (external) part, and bear a lower number of vascular openings on their surface. We believe that our hypothesis adds a new perspective on the evolution of dermal sculpture that does not compete or conflict with those previously proposed.

3. CARBON DIOXIDE ELIMINATION IN VERTEBRATES

(a) *Extant vertebrates*

There is a profound difference between modern fishes and most modern tetrapods in CO_2 elimination and acid–base balance, both in how CO_2 is excreted and in how decreases in body fluid pH are managed. A fundamental shift in these physiological processes must have occurred early in tetrapod evolution, at least by the common ancestor of modern amphibians and amniotes. Our interest here is in how this change might have occurred, and whether early tetrapods used mechanisms that were different from those seen in extant forms as an intermediate condition.

Most fishes have little difficulty eliminating CO_2 [27], and teleosts rely heavily on the gills for physiological mechanisms of pH compensation from acidosis caused by excessive CO_2 accumulation [28]. Because there is approximately 15 times more O_2 in air than a similar volume of water (estimated at 25°C, 1 atm), relatively large gill ventilatory volumes are required (i.e. a high convection requirement) to extract enough oxygen to meet metabolic needs. The result is that nearly all of the CO_2 is washed out of the venous blood at the gills such that a typical fish has CO_2 partial pressure (PCO_2) of the blood of around 2–5 mmHg. Conversely, because of the abundance of oxygen in air, reptiles (i.e. ectothermic amniotes) ventilate their lungs at a comparatively low rate (i.e. a low convection requirement) in comparison with the rate of gill ventilation: thus they have higher blood PCO_2 values between 10 and 30 mmHg, depending on temperature (see [29] for review).

Extant amphibians (lissamphibians) are usually bimodal breathers, relying on buccal pumping to ventilate their lungs as well as a thin, highly vascularized skin for gas exchange, which augments CO_2 elimination. As a result, their blood PCO_2 values are lower than reptiles but higher than fishes, usually between 5 and 15 mmHg. The relative importance of the lungs and skin for eliminating CO_2 depends on factors such as temperature, metabolic rate and season; some small salamanders lack lungs, with all metabolically produced CO_2 eliminated transcutaneously [30]. Extant lungfishes, while they do eliminate some CO_2 by aerial respiration, principally rely on the gills and skin for this purpose even if some species (i.e. the lepidosirenid lungfishes *Protopterus* and *Lepidosiren*) require the lung for oxygen uptake [31].

(b) *Limits on carbon dioxide elimination in early tetrapods*

It is unlikely that the early tetrapods were lissamphibian-like bimodal breathers: they probably had a skin more like that of modern amniotes, albeit not as heavily keratinized as in most reptiles [32], and thus their skin was unlikely to have served as an important avenue for eliminating CO_2. Additionally, the larger body size of many taxa (in comparison with modern amphibians; up to 1 m in length) would result in greater CO_2 accumulation because of surface-area to volume constraints.

Packard [7] proposed three alternative hypotheses for CO_2 elimination in early tetrapods. First, that these tetrapods retained their gills and excreted CO_2 upon returning to the water [6]. Gills are retained in Devonian tetrapods [1] and many aquatic anamniote tetrapods in the Permo-Carboniferous and Triassic also retained fish-like internal gills [33]. Thus, all gill-retaining tetrapods appear to have been primarily aquatic forms: retention of gills does not seem to have been an option for the more terrestrial taxa.

Second, that early tetrapods had amniote-like high rates of ventilation to 'breathe off' more CO_2; however, their ribs were immobile and costal ventilation would have been impossible [8]. A third hypothesis, that the ability to tolerate high levels of CO_2 evolved before the transition to land (see also [34,35]), will be discussed later.

(c) *Defending blood pH when carbon dioxide elimination is impaired*

When the ability of an animal to eliminate CO_2 is impaired, CO_2 accumulates in the animal as carbonic acid, which dissociates to form HCO_3^- and H^+ to decrease body fluid pH. While the actual handling of the CO_2 by different tissues can vary, the end result is a net accumulation of protons in the body fluids, including the extracellular fluid. If the accumulated CO_2 originates from the respiratory processes occurring at the cellular level, such as insufficient ventilation, it is known as respiratory acidosis. A regulated increase in blood HCO_3^- in response to any kind of acidosis is referred to as compensatory metabolic alkalosis.

As mentioned previously, air-breathers have higher blood PCO_2 levels than water-breathers because of the lower convection requirement of their respiratory medium (air). In order to prevent this CO_2 from acidifying their blood, tetrapods have evolved the ability to maintain higher blood HCO_3^- levels. In amniotes, regulation

is accomplished by the kidney, while in amphibians regulation also occurs in the skin and urinary bladder [36].

Lungfishes, which can breathe in both water and air, routinely experience respiratory acidosis when gill ventilation is compromised, such as when aestivating. However, the African lungfish (*Protopterus*) cannot fully compensate its blood pH and shows only small changes in blood HCO_3^- during aestivation [37]. The South American lungfish (*Lepidosiren*) shows incomplete pH compensation and no increase in blood HCO_3^- when subjected to aquatic hypercapnia, even when its gills can be ventilated [38]. Thus, extant lobe-finned fish appear to have limited physiological capacities for acidosis regulation.

Modern amphibians, which breathe primarily air but also may exchange gasses across the skin when submerged in water, are remarkably similar to lungfishes in that they also show either incomplete or no change in blood HCO_3^-, and show incomplete pH compensation with respiratory acidosis [36]. This leads us to conclude, by the application of the extant phylogenetic bracket, that early tetrapods likely shared these physiological limitations with modern air-breathing fish and amphibians, and thus also had a limited capacity to defend their extracellular pH in the face of limited CO_2 elimination.

Any early tetrapod with limits on CO_2 elimination from basal metabolism alone would have even more difficulty doing so when metabolic rate, and therefore CO_2 production rate, was elevated, such as during activity. The situation would be compounded by the higher energetic costs of activity on land, compared with water [13], which would have resulted even greater CO_2 accumulation and respiratory acidosis. It is also likely that the higher metabolic demands on land might have frequently exceeded the ability of the cardiorespiratory system to deliver oxygen to active muscles, so that terrestrial locomotion probably resulted in lactic acid production from anaerobic metabolism. With a limited capacity to compensate extracellular pH under conditions favouring respiratory and probably metabolic acidoses, early tetrapods would have needed to rely on some other buffering means to minimize acidosis and maintain activity.

(d) *Mineralized tissue as a pH buffer in vertebrates*

Overwhelming evidence from recent physiological studies supports a role for mineralized tissue in the buffering of metabolic and respiratory acidosis in ectothermic tetrapods, including frogs [39–41], turtles [42,43] and caiman [44]. Terrestrial frogs subjected to hypercapnia will mobilize calcium carbonate deposits in their endolymphatic lime sacs [39,40], and they also use this source to buffer lactic acidosis from anoxia and exercise [41]. Endochondral bone can also buffer lactic acidosis in amphibians [41] and turtles [45], although some bones, such as the pelvis, scapula and fibula, have been shown to be less effective [45]. Even the turtle's skull, which is dermal bone, does not buffer lactic acidosis as effectively as the shell. A lesser degree of vascularization is most likely the limiting factor in each of these cases.

Turtles show non-renal increases in plasma concentrations of calcium, magnesium and bicarbonate with hypercapnia, which is direct evidence that bone buffers respiratory acidosis in reptiles [42]. The mechanisms by which bone buffers acidosis in reptiles and amphibians appear to involve passive exchange of ions between the bone mineral matrix and the extracellular fluid. Protons generated metabolically or from carbonic acid (from carbon dioxide) exchange with calcium and magnesium in bone, causing the latter to accumulate in the extracellular fluid.

There have been no studies in reptiles and amphibians that suggest a clear histological signal for detecting previous bone buffering episodes, and it is debatable whether one might be able find that would not have a high rate of false negatives. Studies in turtles show that bone contains so much mineral that even under the most extreme lactic acidosis (plasma lactate = 150 mM), relatively large releases of extracellular calcium and magnesium from bone (46 mM and 12 mM, respectively), have no detectable effects on bone mineral content [46]. Thus, it remains unlikely that we would be able to detect a histological signal for this type of physiology in extinct tetrapods.

4. DISCUSSION: MINERALIZED-TISSUE-BUFFERED ACIDOSIS IN EARLY TETRAPODS

We propose that the sculptured dermal bones of early tetrapods, associated with their high degree of vascularization, functioned to buffer the respiratory acidosis that would have resulted from an increased duration on land. These animals likely would have lacked adequate means for CO_2 elimination, such as the capacity to achieve the high ventilation rates made possible by costal aspiration, the ability to lose significant amounts of CO_2 via the skin, or the kidney function necessary to increase blood HCO_3^- concentrations to levels required to fully compensate for respiratory acidosis.

The physiology of some extant terrestrial frogs is especially illuminating here. Lissamphibians usually lack integumental dermal bone; yet the importance of buffering CO_2 is demonstrated by the use in frogs of both endochrondral bone calcium deposits and calcium deposits in their endolymphatic sacs to compensate both respiratory acidosis, caused by elevated CO_2 levels, and lactic acidosis, caused by anoxic submergence and exercise. No such role has been proposed for the osteoderms seen in some frogs, but we note that such species [19] are primarily larger, terrestrial forms (H. Astley 2011, personal communication), which are precisely those forms that would experience difficulties in CO_2 loss.

The pattern of dermal sculpture and of possession of osteoderms in early tetrapods largely accords with our hypothesis that these integumentary structures would have been important for buffering acidosis on land, and that CO_2 loss was a significant problem for these animals. Below we detail various predictions that can be made if our hypothesis is correct, and if the data support the hypothesis.

It is important here to note that the lifestyle of early tetrapods is often difficult to assess (see discussion in [12]). Although the presence of lateral line sulci clearly shows that the animal was mainly aquatic, the absence of such sulci on the bone surface does not necessarily indicate that the lateral line organ was not present in the skin [47]. Further indicators of an aquatic lifestyle are ossified branchial arches and/or branchial dentition [33]. Terrestrial taxa usually have long and robust extremities, and the trunk and tail are rather short. In primarily aquatic taxa, in contrast, the trunk is often elongate, the limbs short and the tail is developed as a

long propulsive organ. Furthermore, the overall degree of ossification of endochondral bones in the postcranial skeleton is often much higher than in aquatic taxa [48]. These criteria are used here to designate early tetrapod taxa as primarily 'aquatic', 'semiterrestrial' or 'terrestrial'.

The hypothesis that sculptured dermal bones are a response to terrestrial hypercapnia, and that they had the function of buffering acidosis, can be tested by predictions as to the correlation of the degree of dermal sculpturing with an aquatic or terrestrial lifestyle.

Prediction 1. Terrestrial early tetrapods have a more pronounced dermal sculpture than primarily aquatic forms. (Note here that terrestriality was derived independently numerous times within these tetrapods, and that some formerly more terrestrial forms became secondarily more aquatic.)

Observations. In tetrapodomorph fishes like *Eusthenopteron*, *Elpistostege* and *Panderichthys*, dermal sculpture is weakly developed and consists of low tubercles and vermiculate ridges [49–51]. In the Devonian stem tetrapods, dermal sculpture is more pronounced than in their fish-like relatives and is rather irregular. Although these forms were primarily aquatic, they were certainly already capable of land excursions and periodically exposed to air [26]. In the basal-most post-Devonian tetrapods, the whatcheeriids, dermal sculpture is almost completely absent in *Whatcheeria*, which can be interpreted as an aquatic animal [52]. In contrast *Pederpes*, which is regarded as more terrestrial than *Whatcheeria*, bears dermal sculpture (although rather weakly developed) [53]. Within temnospondyls (stem amphibians), there is a pronounced trend for largely terrestrial forms like eryopids and dissorophids to have coarse, irregular sculpture [11,12]. In primarily aquatic temnospondyls like stereospondylomorphs, sculpture is not absent, but is normally not as pronounced (ridges and tubercles are lower), and is more regular than in terrestrial forms.

Taxa that do not fit this prediction include the various forms that appear to be aquatic (possessing lateral line sulci) yet that possess dermal armour. These include baphetids, colosteids (both stem tetrapods) and plagiosaurids (temnospondyls). Plagiosaurids, which bear pronounced tubercular dermal sculpture and a covering of osteoderms, were flattened-bodied bottom-dwelling forms, which also showed hypertrophic ossification throughout their entire skeleton that would have acted as ballast [54]. The colosteids also had morphological features such as general flattening, and heavy, thickened dermal scales, indicative of bottom dwelling.

Prediction 2. Dermal sculpturing would be reduced or lost in stem amniote taxa that showed evidence (from rib morphology) of some degree of costal ventilation (a much more efficient way of losing CO_2 than the buccal pumping of modern amphibians, see [8]).

Observations. In 'anthracosaur' stem amniotes (embolomeres, gephyrostegids), dermal sculpture is irregular and often subdued irrespective of a more aquatic or terrestrial mode of life.

Prediction 3. Small terrestrial forms, with surface-area-to-volume ratios similar to that of living amphibians, would lose dermal armour and rely on the skin for CO_2 loss (note that dermal scale loss is also seen today in small semi-terrestrial fish such as mudskippers [55]).

Observations. In the lepospondyls, mostly small-bodied forms, dermal sculpture is often weakly developed or may even be absent. Microsaurs were apparently terrestrial, and their small size would have enabled them to lose CO_2 by diffusion, as in lissamphibians. Evidence of dermal sculpturing is seen only in *Pantylus*, a particularly large microsaur [56]. However, the aquatic diplocaulids have a rather regular sculpture of pits similar to that of stereospondylomorphs [12].

The small terrestrial microsaurs retained thin dermal scales, but scalation was lost in most of the amphibamids, temnospondyls implicated in the origin of lissamphibians [57], and scalation was reduced in the newt-like branchiosaurid temnospondyls [58]. These forms possibly also had a similarly thin skin for gas exchange as do lissamphibians. Note that the branchiosaurid *Apateon* and the amphibamid *Amphibamus grandiceps* have preserved postotic structures interpreted to be calcium-filled endolymphatic sacs, as in some living frogs [59,60], and similar structures can be found in small larvae of the seymouriamorph *Ariekanerpeton* (F. Witzmann 2011, personal observations).

In summary, dermal sculpture is indeed more pronounced in terrestrial early tetrapods. Dermal sculpture is reduced or lost only in those forms that would have been small enough to have been lissamphibian-like bimodal breathers, losing CO_2 through their skin, or in stem amniotes with evidence of costal ventilation.

However, the picture is not always consistent: while the majority of aquatic taxa had less pronounced sculptured dermal bone, a few showed more pronounced sculpturing (e.g. plagiosaurids, colosteids and baphetids), These forms were predominantly bottom-dwelling taxa, with heavily ossified skeletons, and dermal sculpture may have added to this ballast weight. Alternatively, these aquatic forms may have specialized for hypercapnic or hypoxic aquatic environments, as indicated by their flattened body forms, and their integumental features represented an adaptation for carbonic and metabolic acid buffering in this type of environment (see also [35]).

Dermal sculpture occurs also in a few terrestrial basal amniotes, such as most parareptiles (e.g. pareiasaurs and lanthanosuchids), and in the basal eureptile captorhinomorphs (e.g. romeriids [61]). It is possible that these forms were not yet as efficient at costal ventilation as later amniotes. Although derived terrestrial stem amniotes such as *Diadectes* appear to lack dermal armour, the postcranial modifications in early amniotes (e.g. the more consolidated ankle joint) may have resulted in a greater degree of mobility on land, and hence a greater potential for acidosis, especially in larger forms such as these parareptiles. However, sculptured dermal bones are lacking in the synapsids and in more derived eureptiles.

5. CONCLUSIONS

Studies on living tetrapods show that dermal bone has the physiological capacity to buffer acidosis caused by the build-up of CO_2 and lactic acid. We propose that a key function of the dermal bone sculpture associated with strong vascularization that is characteristic of early, basal tetrapods was to buffer CO_2-induced acidosis and perhaps also lactic acidosis induced by periods of anaerobic activity, thus allowing these animals to maintain homeostasis for longer periods of time while on land.

The longer an individual could survive in this new environment, the more it would be able to exploit

terrestrial resources. The pattern of dermal sculpture in the various early tetrapod taxa can be shown to correspond with patterns of terrestrial versus aquatic habits, with terrestrial forms generally having more pronounced sculpture. Terrestrial forms with reduced sculpture were either small stem lissamphibians, where CO_2 loss could be cutaneous, or stem amniotes with morphological evidence of amniote-like costal ventilation.

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REFERENCES

1 Clack, J. A. 2007 Devonian climate change, breathing, and the origin of the tetrapod stem group. *Integr. Comp. Biol.* **47**, 510–523. (doi:10.1093/icb/icm055)

2 Berner, R. A., Beerling, B. J., Dudley, R., Robinson, J. M. & Wildman, R. A. 2003 Phanerozoic atmospheric oxygen. *Annu. Rev. Earth Planet. Sci.* **31**, 105–134. (doi:10.1146/annurev.earth.31.100901.141329)

3 Howell, B. J. 1970 Acid–base balance in transition from water breathing to air breathing. *Fed. Proc.* **29**, 1130–1134.

4 Gans, C. 1970 Respiration in early tetrapods-the frog is red herring. *Evolution* **24**, 723–734. (doi:10.2307/2406552)

5 Gans, C. 1970 Strategy and sequence in the evolution of the external gas exchangers of ectothermal vertebrates. *Forma et Functio* **3**, 61–104.

6 Romer, A. S. 1972 Skin breathing: primary or secondary? *Resp. Physiol.* **14**, 183–192. (doi:10.1016/0034-5687(72)90027-8)

7 Packard, G. C. 1976 Devonian amphibians: did they excrete carbon dioxide via skin, gills, or lungs? *Evolution* **30**, 270–280. (doi:10.2307/2407701)

8 Janis, C. M. & Keller, J. 2001 Modes of ventilation in early tetrapods: coastal aspiration as a key feature of amniotes. *Acta Palaeontol. Pol.* **46**, 137–170.

9 Bystrow, A. P. 1935 Morphologische Untersuchungen der Deckknochen des Schädels der Stegocephalen. 1. Mitteilung. Schädel der Stegocephalen. *Acta Zool. Stockholm* **16**, 65–141. (doi:10.1111/j.1463-6395.1935.tb00664.x)

10 Bystrow, A. P. 1947 Hydrophilous and xerophilous labyrinthodonts. *Acta Zool. Stockholm* **28**, 137–164. (doi:10.1111/j.1463-6395.1947.tb00024.x)

11 Schoch, R. R. 2001 Can metamorphosis be recognised in Palaeozoic amphibians? *Neues Jahrb. Geol. Paläontol. Abh.* **230**, 335–367.

12 Witzmann, F., Scholz, H., Müller, J. & Kardjilov, N. 2010 Sculpture and vascularization of dermal bones, and the implications for the physiology of basal tetrapods. *Zool. J. Linnean Soc. Lond.* **160**, 302–340. (doi:10.1111/j.1096-3642.2009.00599.x)

13 Schmidt-Nielsen, K. 1972 Locomotion: energy cost of swimming, flying, and running. *Science* **77**, 222–228. (doi:10.1126/science.177.4045.222)

14 Dias, E. V. & Richter, M. 2002 On the squamation of *Australerpeton cosgriffi* Barberena, a temnospondyl amphibian from the Upper Permian of Brazil. *An. Acad. Bras. Cienc.* **74**, 477–490. (doi:10.1590/S0001-37652002000300010)

15 Dilkes, D. 2009 Comparison and biomechanical interpretations of the vertebrae and osteoderms of *Cacops aspidephorus* and *Dissorophus multicinctus* (Temnospondyli, Dissorophidae). *J. Vertebr. Paleontol.* **29**, 1013–1021. (doi:10.1671/039.029.0410)

16 Witzmann, F. 2007 The evolution of the scalation pattern in temnospondyl amphibians. *Zool. J. Linnean Soc. Lond.* **150**, 815–834. (doi:10.1111/j.1096-3642.2007.00309.x)

17 Witzmann, F. 2011 Morphological and histological changes of dermal sales during the fish-to-tetrapod transition. *Acta Zool. Stockholm* **92**, 281–302. (doi:10.1111/j.1463-6395.2010.00460.x)

18 Witzmann, F. & Soler-Gijón, R. 2010 The bone histology of osteoderms in temnospondyl amphibians and in the chroniosuchian, *Bystrowiella*. *Acta Zool. Stockholm* **91**, 96–114. (doi:10.1111/j.1463-6395.2008.00385.x)

19 Vickaryous, M. K. & Sire, J.-Y. 2009 The integumentary skeleton of tetrapods: origin, evolution and development. *J. Anat.* **214**, 441–464. (doi:10.1111/j.1469-7580.2008.01043)

20 Zylberberg, L. & Wake, M. H. 1990 Structure of the scales of *Dermophis* and *Microcaecilia* (Amphibia: Gymnophiona) and a comparison to dermal ossifications of other vertebrates. *J. Morphol.* **165**, 41–54. (doi:10.1002/jmor.1052060104)

21 Castanet, J., Francillon-Vieillot, H., de Ricqlès, A. & Zylberberg, L. 2003 The skeletal histology of the Amphibia. *Amphib. Biol.* **5**, 1598–1683.

22 Sire, J.-Y., Donoghue, P. & Vickaryous, M. 2009 Origin and evolution of the integumentary skeleton in non-tetrapod vertebrates. *J. Anat.* **214**, 409–440. (doi:10.1111/j.1469-7580.2009.01046)

23 Cosgriff, J. W. & Zawiskie, J. M. 1979 A new species of the Rhytidosteidae from the *Lystrosaurus* zone and a review of the Rhytidosteoidea. *Palaeontol. Africana* **22**, 1–27.

24 Coldiron, R. W. 1974 Possible functions of ornament in labyrinthodont amphibians. *Occas. Pap. Mus. Nat. Hist. (Lawrence)* **33**, 1–19.

25 Seibert, E. A., Lillywhite, H. B. & Wassersug, R. J. 1974 Cranial co-ossification in frogs: relationship to rate of evaporite water loss. *Physiol. Zool.* **47**, 261–265.

26 Carroll, R. L., Irwin, J. & Green, D. M. 2005 Thermal physiology and the origin of terrestriality in vertebrates. *Zool. J. Linnean Soc. Lond.* **143**, 345–358. (doi:10.1111/j.1096-3642.2005.00151.x)

27 Dejours, P. 1987 Water and air physical characteristics and their physiological consequences. In *Comparative physiology: life in water and on land* (ed. P. Dejours), pp. 3–11. Fidia Research Series, IX. Padova, Italy: Liviana Press.

28 Perry, S. F. & Gilmour, K. M. 2006 Acid–base balance and CO_2 excretion in fish: unanswered questions and emerging models. *Resp. Physiol. Neurobi.* **154**, 199–215. (doi:10.1016/j.resp.2006.04.010)

29 Burton, R. F. 2002 Temperature and acid–base balance in ectothermic vertebrates: imidazole alphastat hypotheses and beyond. *J. Exp. Biol.* **205**, 3587–3600.

30 Full, R. J. 1986 Locomotion without lungs: energetic and performance of a lungless salamander. *Am. J. Physiol.* **251**, R775–R780.

31 Lenfant, C. & Johansen, K. 1968 Respiration in the African lungfish *Protopterus aethiopicus*. I. Respiratory properties of blood and normal patterns of breathing and gas exchange. *J. Exp. Biol.* **49**, 437–452.

32 Maddin, H. C., Musat-Marcu, S. & Reisz, R. R. 2007 Histological microstructure of the claws of the African Clawed Frog, *Xenopus laevis* (Anura: Pipidae): implications for the evolution of claws in tetrapods. *J. Exp. Biol.* **308B**, 259–268. (doi:10.1002/jez.b.21145)

33 Schoch, R. R. & Witzmann, F. 2011 Bystrow's paradox: gills, fossils, and the fish-to-tetrapod transition. *Acta Zool. Stockholm* **92**, 251–265. (doi:10.1111/j.1463-6395.2010.00456.x)

34 Ultsch, G. R. 1996 Gas exchange, hypercarbia and acid–base balance, paleoecology, and the evolutionary

transition from water-breathing to air-breathing among vertebrates. *Palaeogeogr. Palaeocl.* **123**, 1–27. (doi:10.1016/0031-0182(96)00121-6)
35 Ultsch, G. R. 2011 Metabolism, gas exchange, and acid–base balance of giant salamanders. *Biol. Rev.* (doi:10.1111/j.1469-185X.2011.00211.x)
36 Toews, D. P. & Boutilier, R. G. 1986 In *Acid–base regulation in the Amphibia. Acid–base regulation in animals* (ed. N. Heisler), pp. 265–308. New York, NY: Elsevier.
37 DeLaney, R. G., Lahiri, S., Hamilton, R. & Fishman, A.P. 1977 Acid–base balance and plasma composition in the aestivating lungfish (*Protopterus*). *Am. J. Physiol.* **232**, R10–R17.
38 Sanchez, A. P., Giusti, H., Bassi, M. & Glass, M. L. 2005 Acid–base regulation in the South American lungfish *Lepidosiren paradoxa*: effects of prolonged hypercarbia on blood gases and pulmonary ventilation. *Physiol. Biochem. Zool.* **78**, 908–915. (doi:10.1086/432859)
39 Simkiss, K. 1968 Calcium and carbonate metabolism in the frog (*Rana temporaria*) during respiratory acidosis. *Am. J. Physiol.* **214**, 627–634.
40 Tufts, B. L. & Toews, D. P. 1985 Partitioning of regulatory sites in *Bufo marinus* during hypercapnia. *J. Exp. Biol.* **119**, 199–209.
41 Warren, D. E. & Jackson, D. C. 2005 The role of mineralized tissue in the buffering of lactic acid during anoxia and exercise in the leopard frog *Rana pipiens*. *J. Exp. Biol.* **208**, 1117–1124. (doi:10.1242/jeb.01490)
42 Silver, R. B. & Jackson, D.C. 1986 Ionic compensation with no renal response to chronic hypercapnia in *Chrysemys picta bellii*. *Am. J. Physiol.* **251**, 1228–1234.
43 Jackson, D. C. 2000 How a turtle's shell helps it survive prolonged anoxic acidosis. *News Physiol. Sci.* **15**, 181–185.
44 Jackson, D. C., Andrade, D. & Abe, A. 2003 Lactate sequestration by osteoderms of the broad-nose caiman, *Caiman latirostris*, following capture and forced submergence. *J. Exp. Biol.* **206**, 3601–3606. (doi:10.1242/jeb.00611)
45 Davis, E. C. & Jackson, D. C. 2007 Lactate uptake by skeletal bone in anoxic turtles, *Trachemys scripta*. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **146**, 299–304. (doi:10.1016/j.cbpa.2006.10.034)
46 Jackson, D. C., Crocker, C. E. & Ultsch, G. R. 2000 Bone and shell contribution to lactic acid buffering of submerged turtles *Chrysemys picta bellii* at 3°C. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **278**, R1564–R1571.
47 Laurin, M., Girondot, M. & Loth, M. M. 2004 The evolution of long bone microanatomy and lifestyle in lissamphibians. *Paleobiology* **30**, 589–613. (doi:10.1666/0094-8373(2004)030<0589:TEOLBM>2.0.CO;2)
48 Schoch, R. R. 2002 The evolution of metamorphosis in temnospondyls. *Lethaia* **35**, 309–327. (doi:10.1111/j.1502-3931.2002.tb00091.x)
49 Jarvik, E. 1980 *Basic structure and evolution of vertebrates*. London, UK: Academic Press.
50 Schultze, H.-P. & Arsenault, M. 1985 The panderichthyid fish *Elpistostege*: a close relative of tetrapods? *Palaeontology* **28**, 293–309.
51 Vorobyeva, E. I. & Schultze, H. P. 1991 Description and systematics of panderichthyid fishes with comments on their relationship to tetrapods. In *Origins of the higher groups of tetrapods, controversy and consensus* (eds H. P. Schultze & L. Trueb), pp. 68–109. Ithaca, NY: Comstock Publishing Associates, Cornell University Press.
52 Lombard, R. E. & Bolt, J. R. 1995 A new primitive tetrapod, *Whatcheeria deltae*, from the Lower Carboniferous of Iowa. *Palaeontology* **38**, 471–495.
53 Clack, J. A. & Finney, S. 2005 *Pederpes finneyae*, an articulated tetrapod from the Tournaisian of western Scotland. *J. Syst. Palaeontol.* **2**, 311–346. (doi:10.1017/S1477201904001506)
54 Schoch, R. R. & Witzmann, F. 2011 Cranial morphology of the plagiosaurid *Gerrothorax pulcherrimus* as an extreme example of evolutionary stasis. *Lethaia*. (doi:10.1111/j.1502-3931.2011.00290.x)
55 Park, J. Y. 2002 Structure of the skin of an air-breathing mudskipper, *Periophthalmus magnuspinnatus*. *J. Fish Biol.* **60**, 1543–1550. (doi:10.1006/jfbi.2002.2014)
56 Carroll, R. L. 1998 Order Microsauria. In *Encyclopedia of paleoherpetology, vol. 1: Lepospondyli* (ed. P. Wellnhofer), pp. 1–72. München, Germany: Verlag Dr. Friedrich Pfeil.
57 Anderson, J. S., Reisz, R. R., Scott, D., Fröbish, N. S. & Sumida, S. S. 2008 A stem batrachian from the Early Permian of Texas and the origin of frogs and salamanders. *Nature* **453**, 515–518. (doi:10.1038/nature06865)
58 Boy, J. A. 1993 Synopsis of the tetrapods from the Rotliegend (Lower Permian) in the Saar-Nahe Basn (SW-Germany). In *New research on Permo-Carboniferous faunas*, vol. 29 (ed. U. Heidtke), pp. 155–169. Bad Dürtzheim, Germany: Selbstverlag de Pollichia.
59 Boy, J. A. 1974 Die Larven der rhachitomen Amphibien (Amphibia: Temnospondyli; Karbon—Trias). *Paläont. Z.* **48**, 236–282.
60 Milner, A. R. 1982 Small temnospondyl amphibians from the Middle Pennsylvanian of Illinois. *Palaeontology* **25**, 635–664.
61 Carroll, R. L. & Baird, D. 1972 Carboniferous stem-reptiles of the family Romeriidae. *Bull. Mus. Comp. Zool.* **143**, 321–364.

Dermal bone sculpture in early tetrapods: external morphology, histology and possible functions

Appendix 4

Witzmann, F. 2010. A skull fragment of a Devonian tetrapod in the collection of the Museum für Naturkunde Berlin showing a unique lateral line morphology. – Fossil Record 13: 297–302.

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WILEY-VCH museum für naturkunde

A skull fragment of a Devonian tetrapod with a unique lateral line morphology in the collection of the Museum für Naturkunde Berlin

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Abstract

A dermal bone from the late Famennian of Ketleri in Latvia, identified as a probable tetrapod postorbital by Oleg Lebedev and stored in the Museum für Naturkunde Berlin, is described in detail. Its tetrapod status is confirmed based on the dermal sculpture consisting of polygonal pits and radially aligned ridges and furrows. The sculpture resembles that of Devonian tetrapods but is nevertheless not as regular as in most post-Devonian forms. The bone can be designated as a postorbital because of its concave anterior margin, the lateral line that shows no bifurcation, and the ossification centre that is located in the dorsal portion of the bone. The lateral line (i.e., the postorbital branch of the infraorbital line) forms an open, deep sulcus in the ventral portion of the postorbital but is enclosed within the bone in the dorsal portion and opens through pores to the surface. This morphology of the postorbital branch is unique among basal tetrapods. The bone might belong to the tetrapod *Ventastega curonica* Ahlberg et al., 1994 that is known from the same strata at Ketleri, however, since the postorbital is unknown in this taxon, this cannot be stated with certainty.

Introduction

In the original description of the Devonian tetrapod *Ventastega curonica* Ahlberg et al., 1994, Oleg Lebedev mentioned his finding of an uncatalogued, presumed postorbital bone from the Late Devonian of Latvia in the collection of fossil fishes in the Museum für Naturkunde in Berlin (Ahlberg et al. 1994). The bone bears a dermal sculpture of radially arranged ridges and furrows and is crossed by a partially enclosed lateral line canal. This specimen was collected at the right bank of the Venta river (former German name: Fluss Windau) near Ketleri hamlet by Walter Gross in 1931 together with a large amount of further vertebrate remains. Two years later, Gross (1933) described several of his findings that mainly consisted of 'agnathans', placoderms, chondrichthyans, actinopterygians and fish-like sarcopterygians. However, he neither described nor mentioned the postorbital bone from Ketleri. Ahlberg et al. (1994) gave a brief description of this bone, but did not provide an illustration. Based on the 'tetrapod-like' dermal sculpture of this bone, these authors suspected that it probably belongs to a tetrapod, possibly to *Ventastega*, remains of which have also been found at Ketleri locality. Because of the uncertainty of its taxonomic affinities, Ahlberg et al. (1994) did not incorporate this bone in their reconstruction of the skull of *Ventastega*.

The Ketleri Formation, from which this bone is derived, is late Famennian (Late Devonian) in age. It is composed of unconsolidated sand, sandstones, clays and dolomitic marls, and was probably deposited in a shallow basin under brackish conditions (Lukševičs & Župins 2004). Lyarskaja & Savvaitova (1974) divided the Ketleri Formation into three members with the Ketleri locality belonging to the upper member, which is named Varkali Member. A diverse vertebrate fauna has been excavated at the Venta river near Ketleri (Gross 1933; Lukševičs 1991, 2001; Ahlberg et al. 1994) that comprises the placoderm *Bothriolepis ciecere* Lyarskaja, 1974 (in Lyarskaja & Savvaitova 1974), the acanthodians *Devononchus tenuispinus* (Gross, 1933) and *D. ketleriensis* Gross, 1947, the porolepiform *Holoptychius* cf. *nobilissimus* Agassiz, 1839, the osteolepiforms *Cryptolepis grossi* Vorobyeva, 1975 and *Glyptopomus bystrowi* (Gross, 1941), the dipnoan *Orlovichthys* cf. *limnatis* Krupina, 1980, the enigmatic *Ventalepis ketleriensis* Schultze, 1980, which is a possible holoptychiid (Schultze 1980), and the tetrapod *Ventastega curonica*. Ahlberg et al. (1994) pointed out that a large tristichopterid (eusthenopterid) probably also belongs to the fauna at Ketleri site.

Since the first mentioning of the postorbital bone from Ketleri by Ahlberg et al. (1994), the specimen has got an inventory number but was not assigned to any vertebrate group. The present study gives a detailed description of this element for the first time and aims to assess the characters that justify its tetrapod nature.

In the present paper, the apomorphy-based definition of Tetrapoda is used, i.e., Tetrapoda is defined as a clade that encompasses those vertebrates, which have digitized limbs rather than paired fins (see Anderson 2002, and references therein). This apomorphy-based definition considers the historical usage of the term Tetrapoda and reflects its etymological meaning. An apomorphy-based Tetrapoda is monophyletic and the homology of its key-apomorphy, the limb with digitized manus and pes, has been demonstrated (J. S. Anderson in Laurin & Anderson 2002). In contrast, a phylogenetic definition of Tetrapoda would either exclude several fossil taxa, which definitively possess digitized limbs (crown-group definition), or would include many sarcopterygians, which possess fins rather than limbs (total-group definition). A further challenge of the phylogenetic definition of Tetrapoda is that there is still no consensus concerning the composition of the tetrapod crowngroup and the identity of the living sistergroup of Tetrapoda (Ahlberg & Clack 1998, and references therein).

Material

The specimen is stored under inventory number MB.f.18028 in the collection for fossil fishes of the Museum für Naturkunde Berlin and consists of an isolated dermal bone fragment, which is almost completely freed from the surrounding sediment matrix. Attached remnants of the bright sandstone can be found only in some of the pits of the sculptured external bone surface.

Description of MB.f.18028

In the following description, the anatomical terms of location (dorsal, ventral, anterior, posterior) refer to the interpretation that this bone is a right postorbital (see discussion). This applies also to the names of the presumed neighbouring bones of this element. The specimen is a flattened dermal bone of elongate, quadrangular outline with a gently tapering ventral margin (Figs 1, 2). It measures 34 mm in dorsoventral extension and has a maximum antero-posterior length of 18 mm. In its dorsal portion, the thickness of the bone reaches its maximum of 4.5 mm, whereas it thins out in a ventral direction where it measures slightly less than 2 mm in its thinnest part. An exception is the anterior (i.e., orbital) margin, that almost retains its thickness also in the ventral portion of the bone. The orbital margin is well preserved. At most of its length, it is rather straight; in its dorsal portion, it turns abruptly in an anterior direction, whereas in the ventral part, the anterior curvature proceeds more gently. Thus, the concave orbital margin appears somewhat angled rather than evenly rounded. The thickened dorsal margin of the bone is straight in its anterior two thirds, before it slopes slightly posteroventrally. The anterior two thirds of the margin probably formed a suture with the postfrontal, whereas the posterior portion might have sutured with an intertemporal or a supratemporal. At least the anterior portion of the dorsal margin exhibits no sutural interdigitations, but a shallow furrow runs antero-posteriorly on the edge, as already recognized by Ahlberg et al. (1994). Thus, the sutural connection with the adjacent dorsal bone (probably the postfrontal) must have been rather straight, and Ahlberg et al. (1994) did not rule out that the dorsal suture might have been kinetic. The original posterior margin of the bone is not preserved since the posterior portion has broken off, so that the specimen is delimited posteriorly by a rather straight edge. The ventral margin of the bone is slightly abraded, but probably corresponds to the original suture with the ventrally attaching bone (presumably the jugal).

The external (superficial) surface of the bone is conspicuously sculptured by ridges, pits, and furrows. Mainly polygonal pits enclosed by ridges can be found in the posterodorsal region, from which ridges and elongate pits and grooves radiate and are directed anteroventrally and ventrally (Figs 1A, 2A). According to Bystrow (1935), the region of a dermal bone with polygonal sculpture usually represents its ossification centre, which in specimen MB.f.18028 is therefore located in its posterodorsal portion. This centre, however, is not completely preserved since the posterior break runs right through it. Overall, the dermal sculpture of the bone appears rather irregular because the pits differ conspicuously in size and shape, and the sculptural ridges and their 'nodal points' (i.e., the points of intersection in which the sculptural ridges meet) show great variability in height and width. The ridges may be broadly rounded or sharply edged dorsally. Each pit contains at least one vascular opening (i.e., the opening of a large vascular canal) on its bottom. As common in sculptured dermal bones of basal tetrapods (Witzmann et al. in press), these canals are directed approximately perpendicular to the bone surface in the polygonal pits of the ossification centre, but are directed obliquely to the surface and aligned rather parallel to the anteroventrally and ventrally running sculptural ridges of the more ventral region. Apart from these vascular openings, there are numerous tiny pores distributed all over the bone surface, both in the pits and furrows, and on the sculptural ridges. In temnospondyls, Bystrow (1935) associated such pores on the dermal sculpture with a network of capillaries within the bone, which he designated as the '*Rete vasculosum*'. Whereas the external surface is rather plane in the dorsal half of the bone, it is slightly concave in its ventral half. This concave area is delimited anteriorly by the open lateral line sulcus (see below) and the thickened orbital margin.

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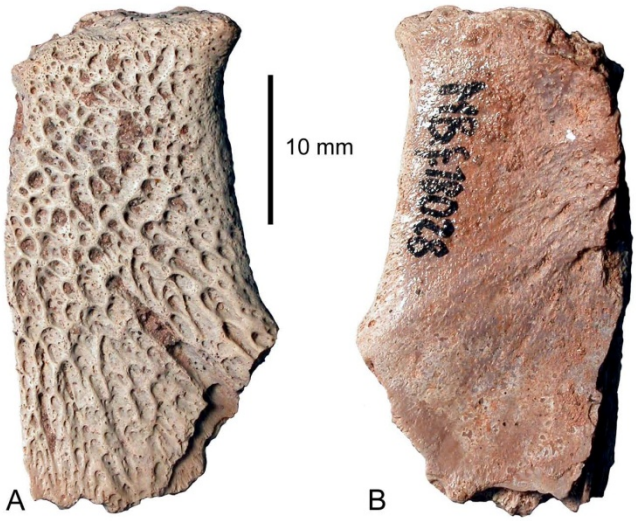

Figure 1. Right postorbital of an unidentified tetrapod from the late Famennian (Late Devonian) of Ketleri, Latvia, stored in the Museum für Naturkunde Berlin under inventory number MB.f.18028. **A.** External view; **B.** Internal view.

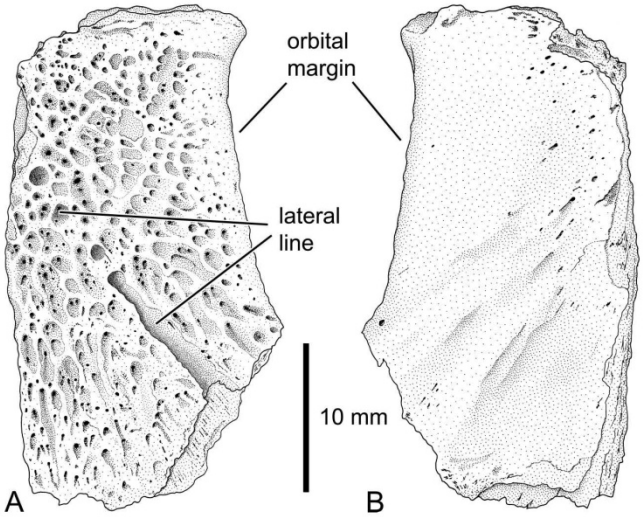

Figure 2. Drawing of right postorbital MB.f.18028 from the late Famennian (Late Devonian) of Ketleri, Latvia. **A.** External view; **B.** Internal view.

A straight, deeply impressed lateral line sulcus is present in the ventral portion of the bone that runs from its anteroventral edge, close to the orbital margin, in a posterodorsal direction (Figs 1A, 2A). Where the infilling of sandstone matrix is removed, it is visible that the bottom of the sulcus is smooth. After approximately 10 mm, the sulcus narrows before it ends after 2 mm in a circular foramen that has a diameter of about 1 mm. Three further foramina can be discerned and are aligned in a row, forming the posterodorsal continuation of the sulcus. These foramina can be differentiated from pits of the dermal sculpture by their more rounded shape.

The internal (deep) surface of the bone is mostly smooth (Figs 1B, 2B). Several vascular canals open to the surface in the posterodorsal portion and are directed anteroventrally and ventrally. In this region, the bone surface shows a gentle upturn that constitutes approximately the dorsal half of the posterior portion.

Discussion

Identification of the bone

Ahlberg et al. (1994) suggested that the bone under study probably represents a postorbital but did not dis-

cuss this issue any further. The postorbital interpretation is followed here. The lateral line canal does not bifurcate, which renders an identification as a jugal implausible. Also the location of the ossification centre of the bone as indicated by the pattern of dermal sculpture, supports the assignment of the bone as a postorbital. The ossification centre is located at one end of the bone (interpreted here as the dorsal portion), from which the radially arranged sculpture fans out. A similar pattern was described in the isolated postorbital of an undetermined tetrapod (?*Tulerpeton*) from Devonian rocks of the Tula Region, Russia (Lebedev & Clack 1993), and in the same bone of an undetermined Devonian tetrapod from Red Hill, Pennsylvania, USA (Daeschler et al. 2009, fig. 5a). In *Acanthostega*, the polygonal sculpture is likewise confined to the dorsal portion of the postorbital (Clack 2003, fig. 1). In contrast, if the bone under study represented a jugal, the ossification centre with polygonal pits would be located more at mid-length along the orbital margin and send out radial furrows and ridges towards both ends. Furthermore, the bone from Ketleri is similar to the postorbital from Tula Region in that the bone is thickened dorsally and becomes thinner in ventral direction. Also, the suture with the postfrontal is similarly smooth in the Tula specimen and might be associated with a kinetic junction between the cheek and the skull table (Lebedev & Clack 1993).

Tetrapod nature of the bone

Ahlberg et al. (1994) stated that the dermal bone from Ketleri probably belongs to a tetrapod based on the tetrapod-type dermal sculpture. This assumption is followed here. Godfrey (1989, p. 127) considered dermal sculpture that 'consists of deep polygonal pits or troughs surrounded by raised ridges' as a tetrapod autapomorphy, and this type of sculpture is found on the external surface of the bone under study. Its irregular sculptural pattern closely resembles that of *Ventastega* and the undetermined Devonian tetrapod from Tula (personal observations). In contrast, the sculptural pattern of most post-Devonian tetrapods like temnospondyls or seymouriamorphs is more regular in that the shape and size of the pits and the height and width of the sculptural ridges generally do not show a correspondingly broad variation (Witzmann et al. in press). Unlike the studied bone, the fish-like sarcopterygians that co-occur in Ketleri, i.e., the porolepiform *Holoptychius* (Jarvik 1972), the 'osteolepid' *Glyptopomus bystrowi* (Gross 1941; Vorobyeva 1962), and tristichopterids (Jarvik 1944) have a tubercular or vermiculate dermal sculpture. The osteolepiform *Cryptolepis grossi*, which was also found at Ketleri site, has cosmine-covered dermal bones (Vorobyeva 1975). Furthermore, in porolepiforms (Jarvik 1972) and osteolepiforms (Jarvik 1944), the lateral lines, which are enclosed in bone, have numerous side branches, whereas in tetrapods, the enclosed canals open via unbranching tubes to the bone surface (Säve-Söderbergh 1932). No side branches are visible in the lateral line of the bone under study. Its tetrapod assignment is further supported by the gentle curvature of the orbital margin that indicates a proportionally large orbit, which is typical for early tetrapods (Coates & Clack 1995; Ahlberg 1998).

Lateral line

In most early tetrapods, the lateral line organ was located at least partially in open sulci on the surface of dermal skull bones, whereas in their fish-like relatives, they ran in true canals within the bone and opened to the surface through pores (Clack 2002a). If the interpretation is correct that the bone from Ketleri is a postorbital, then the lateral line canal represents the postorbital part of the infraorbital line. It consists of an open, but deep sulcus in the ventral portion of the bone and continues in the dorsal part as a row of pores (three single pores and one pore at the termination of the sulcus; see Figs 1A, 2A). In Devonian tetrapods from which the postorbital is known, the openings of the postorbital lateral line are restricted to the ventral portion of the bone, either as a continuous sulcus or as a row of pores (Fig. 3). However, the line may continue as a closed canal to the dorsal edge of the bone (Jarvik 1996; Ahlberg 1998). In *Acanthostega* and *Greererpeton*, the postorbital line is developed as an open sulcus in the more ventral part of the postorbital similar to the Ketleri specimen (Figs 3E, F); this is also the case in the isolated postorbital from Red Hill. However, the line ends in the region of the ossification centre in these taxa (Clack 2002b; Smithson 1982; Daeschler et al. 2009). The isolated tetrapod postorbital bone from the Late Devonian of Scat Craig in Scotland has a lateral line that is enclosed within the bone (Ahlberg 1998). It opens via pores to the surface in the ventral portion (Fig. 3C), but is completely closed in the dorsal part and is visible as a large opening on the dorsal edge of the bone. A similar situation is present in *Ichthyostega* (Fig. 3B; Säve-Söderbergh 1932). The postorbital from Ketleri is unique among Devonian tetrapods because its lateral line continues in the dorsal portion as an enclosed canal *plus* pores (Fig. 3D). In contrast to tetrapods, the postorbital line is enclosed in bone in the fish-like sarcopterygians *Panderichthys* (Vorobyeva & Schultze 1991) and *Tiktaalik* (Fig. 3A; Daeschler et al. 2006), and is visible on the bone surface both on the dorsal and ventral portion as a sensory pore line. Therefore, the pores on the dorsal portion of the Ketleri specimen might be interpreted as a plesiomorphic character. However, the presence of an open lateral line sulcus in the Ketleri specimen is a character that is more 'tetrapod-like' than the enclosed lines of *Ichthyostega* (Säve-Söderbergh 1932).

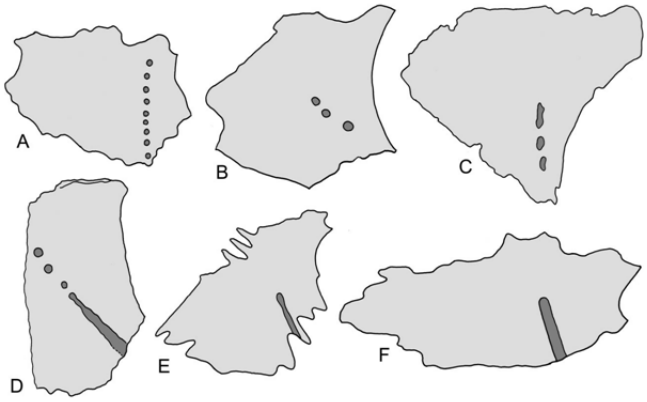

Figure 3. Schematic drawings of postorbitals in early tetrapods and *Tiktaalik*, not to scale. The lateral line sulci and pores, respectively, are held in dark grey. The orbital margin (i.e. anterior) is on the right; to facilitate comparisons, drawings A and C are reversed. **A.** *Tiktaalik*, a Late Devonian tetrapodomorph fish (after Daeschler et al. 2006); **B.** *Ichthyostega*, a Late Devonian tetrapod (after Säve-Söderbergh 1932); **C.** Tetrapod postorbital fragment from the Late Devonian of Scat Craig, Scotland (after Ahlberg 1998); **D.** Ketleri postorbital; **E.** *Acanthostega*, a Late Devonian tetrapod (after Clack 2003); **F.** *Greererpeton*, an Early Carboniferous tetrapod (after Smithson 1982).

Conclusions

The following characters identify the bone from Ketleri as a tetrapod dermal bone: (1) the tetrapod-type dermal sculpture on the external bone surface; (2) the lateral line is partially developed as an open sulcus, and the enclosed portion opens via unbranching tubes to the bone surface; (3) the gentle curvature of the orbital margin suggests a proportionally large orbit as common in early tetrapods, in contrast to the proportionally smaller orbits of fishlike sarcopterygians. This dermal bone can be assigned as a postorbital and not as a jugal for the following reasons: (1) the lateral line canal does not bifurcate; (2) the ossification centre is located at one end of the bone. The lateral line morphology of this postorbital differs from that of all other known early tetrapods in that it consists of an open sulcus in one portion of the bone, whereas it is enclosed in the other portion and opens to the bone surface via pores. As suggested by Ahlberg et al. (1994), this specimen could belong to the Devonian tetrapod *Ventastega curonica*, which has been found in the Ketleri Formation both at Ketleri and Pavāri on the Ciecere River in Latvia. This assignment cannot be stated with certainty since a postorbital that can definitively be attributed to *Ventastega*, has not been found so far (Ahlberg et al. 1994, 2008). Interestingly, Ahlberg et al. (1994) reported an isolated fragment of a lower jaw from Ketleri, which probably belongs to a second tetrapod taxon, indicating that at least two tetrapods were present in the Ketleri fauna. Thus the postorbital from Ketleri is most suitably described as an undetermined Devonian tetrapod.

Acknowledgements

I want to thank Oleg Lebedev (Paleontological Institute, Moscow) and Ivars Zupiņš (Latvian Museum of Natural History, Riga) for access to the collections of *Ventastega* and other Devonian vertebrates under their care. The reviews of Nadia Fröbisch (Chicago), Marcello Ruta (Bristol), Rainer Schoch (Stuttgart), and Hans-Peter Schultze (Lawrence) helped to improve the manuscript. Henning Scholz (Berlin) is acknowledged for taking the photographs, and Johannes Müller (Berlin) for helpful comments on the manuscript. The Deutsche Forschungsgemeinschaft is thanked for financial support (DFG-grant "Dermal bone sculpture in basal tetrapods").

References

Agassiz, L. 1839. Fishes of the Upper Ludlow Rock. *In* Murchison, R. I. (ed.). The Silurian System. Vol. 2. John Murray, London: pp. 605–607.

Ahlberg, P. E. 1998. Postcranial stem-tetrapod remains from the Devonian of Scat Craig, Morayshire, Scotland. – Zoological Journal of the Linnean Society 122: 99–141.

Ahlberg, P. E. & Clack, J. A. 1998. Lower jaws, lower tetrapods – a review based on the Devonian genus *Acanthostega*. – Transactions of the Royal Society of Edinburgh: Earth Sciences 89: 11–46.

Ahlberg, P. E., Lukševičs, E. & Lebedev, O. 1994. The first tetrapod finds from the Devonian (Upper Famennian) of Latvia. – Philosophical Transactions of the Royal Society of London B 343: 303–328.

Ahlberg, P. E., Clack, J. A., Lukševičs, E., Blom, H. & Zupiņš, I. 2008. *Ventastega curonica* and the origin of tetrapod morphology. – Nature 453: 1199–1204.

Anderson, J. S. 2002. Use of well-known names in phylogenetic nomenclature: A reply to Laurin. – Systematic Biology 51: 822–827.

Bystrow, A. P. 1935. Morphologische Untersuchungen der Deckknochen des Schädels der Stegocephalen. 1. Mitteilung. Schädel der Stegocephalen. – Acta Zoologica (Stockholm) 16: 65–141.

Clack, J. A. 2002a. Gaining ground. The origin and evolution of tetrapods. Indiana University Press, Bloomington and Indianapolis.

Clack, J. A. 2002b. The dermal skull roof of *Acanthostega gunnari*, an early tetrapod from the Late Devonian. – Transactions of the Royal Society of Edinburgh: Earth Sciences 93: 17–33.

Clack, J. A. 2003. A revised reconstruction of the dermal skull roof of *Acanthostega gunnari*, an early tetrapod from the Late Devonian. – Transactions of the Royal Society of Edinburgh: Earth Sciences 93: 163–165.

Coates, M. I. & Clack, J. A. 1995. Romer's gap: tetrapod origins and terrestriality. – Bulletin du Muséum National d'Histoire Naturelle 17: 373–388.

Daeschler, E. B., Shubin, N. H. & Jenkins, F. A. Jr. 2006. A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. – Nature 440: 757–763.

Daeschler, E. B., Clack, J. A. & Shubin, N. H. 2009. Late Devonian tetrapod remains from Red Hill, Pennsylvania, USA: how much diversity? – Acta Zoologica (Stockholm) 90 (Issue s1): 306–317.

Godfrey, S. J. 1989. The postcranial skeletal anatomy of the Carboniferous tetrapod *Greererpeton burkemorani* Romer 1969. – Philosophical Transactions of the Royal Society of London B 323: 75–133.

Gross, W. 1933. Die Fische des baltischen Devons. – Palaeontographica A 69: 1–74.

Gross, W. 1941. Über den Unterkiefer einiger devonischer Crossopterygier. – Abhandlungen der Preußischen Akademie der Wissenschaften 1941: 1–51.

Gross, W. 1947. Die Agnathen und Acanthodier des obersilurischen Beyrichienenkalks. – Palaeontographica A 96: 91–161.

Jarvik, E. 1944. On the dermal bones, sensory canals and pit-lines of the skull in *Eusthenopteron foordi* Whiteaves, with some remarks on *E. säve-söderberghi* Jarvik. – Kungliga Svenska Vetenskapsakademiens Handlingar (3) 21: 1–48.

Jarvik, E. 1972. Middle and Upper Devonian Porolepiformes from East Greenland with special reference to *Glyptolepis groenlandica* n. sp. – Meddelelser om Grønland 187: 1–307.

Jarvik, E. 1996. The Devonian tetrapod *Ichthyostega*. – Fossils and Strata 40: 1–213.

Krupina, N. I. 1980. Novyy rod dipnoy iz famena tsentralnogo devonskogo polya. – Paleontologicheskiy Zhurnal 1980 (3): 140–143.

Laurin, M. & Anderson, J. S. 2004. Meaning of the name Tetrapoda in the scientific literature: an exchange. – Systematic Biology 53: 68–80.

Lebedev, O. & Clack, J. A. 1993. Upper Devonian tetrapods from Andreyevka, Tula Region, Russia. – Palaeontology 36: 721–734.

Lukševičs, E. 1991. Bothriolepids of the Ketleri Beds of the Upper Devonian of Latvia (Pisces, Placodermi). – Daba un muzejs 3: 38–50 [In Russian].

Lukševičs, E. 2001. Bothriolepid antiarchs (Vertebrata, Placodermi) from the Devonian of the north-western part of the East European Platform. – Geodiversitas 23: 489–609.

Lukševičs, E. & Zupiņš, I. 2004. Sedimentology, fauna and taphonomy of the Pavāri site, Late Devonian of Latvia. – Acta Universitatis Latviensis 679: 99–119.

Lyarskaja, L. A. & Savvaitova, L. S. 1974. Structure and ichthyofauna of the Ketleri formation of Latvia. *In* Afanasyev, B. L., Volkolakov, F. K., Kuršs, V. M., Lunsh, A. Y., Sorokin, V. S. & Ulst, R. Z. (eds). Regionalnaya geologia Pribaltiki. Zinatne, Riga: pp. 90–106.

Säve-Söderbergh, G. 1932. Preliminary note on Devonian stegocephalians from East Greenland. – Meddelelser om Grønland 94: 1–107.

Schultze, H.-P. 1980. Crossopterygier-Schuppen aus dem obersten Oberdevon Lettlands (Osteichthyes, Pisces). – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 1985: 215–228.

Smithson, T. R. 1982. The cranial morphology of *Greererpeton burkemorani* Romer (Amphibia: Temnospondyli). – Zoological Journal of the Linnean Society 76: 29–90.

Vorobyeva, E. I. 1962. Rhizodont crossopterygian fishes of the Main Devonian Field of the USSR. – Trudy Palaeontologicheskogo Instituta 94: 1–139 [In Russian].

Vorobyeva, E. I. 1975. An osteolepid crossopterygian from the Ketleri Formation of Latvia. *In* Grigelis A. A. (ed.). Fauna and Stratigraphy of the Palaeozoic and Mesozoic of Baltics and Byelorussia. Mintis, Vilnius: pp. 233–237.

Vorobyeva, E. I. & Schultze, H.-P. 1991. Description and systematics of panderichthyid fishes with comments on their relationship to tetrapods. *In* Schultze, H.-P. & Trueb, L. (eds). Origins of higher groups of tetrapods. Comstock Publishing Associates, Ithaca: pp. 68–109.

Witzmann, F., Scholz, H., Müller, J. & Kardjilov, N. In press. Sculpture and vascularization of dermal bones, and the implications for the physiology of basal tetrapods. – Zoological Journal of the Linnean Society.

Histology and external structure of osteoderms in early tetrapods

Appendix 5

Witzmann, F., Schoch, R. R. & Maisch, M. 2008. A relict basal tetrapod from Germany: first evidence of a Triassic chroniosuchian outside Russia. – Naturwissenschaften 95: 67–72.

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DOI 10.1007/s00114-007-0291-6

SHORT COMMUNICATION

A relict basal tetrapod from Germany: first evidence of a Triassic chroniosuchian outside Russia

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Abstract Chroniosuchians are basal tetrapods nesting within the paraphyletic anthracosaurs and were so far only well known from the Permian and Triassic of Russia. In this study, we present evidence for their existence in the upper Middle Triassic of Germany, based on diagnostic osteoderms and vertebrae from the Kupferzell and Vellberg localities in southern Germany. The finds are most similar to *Synesuchus*, a Middle Triassic bystrowianid chroniosuchian from the Northern Ural Pechora region. They demonstrate that by Middle Triassic time, chroniosuchians were much more widespread than previously thought.

Keywords Bystrowianidae · Chroniosuchia · Germany · Keuper · Triassic

Introduction

The Lower Keuper deposits of southern Germany rank among the richest Triassic Fossillagerstätten in the world and since the discovery of the vast Kupferzell assemblage in 1977 have yielded numerous new species of bony fishes, temnospondyl amphibians, and reptiles of diverse clades (Gower 1999; Schoch 1999, 2002, 2006). In this paper, we report the most unexpected and erratic element of that fauna, which represents a relict from deep time: a chroniosuchian basal tetrapod.

Chroniosuchians form typical components of Upper Permian faunas in European Russia and were aquatic, piscivorous non-amniotic tetrapods that superficially resemble extant varanids in proportions (Ivakhnenko and Tverdokhlebova 1980; Novikov et al. 2000). Probably, chroniosuchians are closely related to the Embolomeri within the paraphyletic anthracosaurs (Laurin 2000; Novikov et al. 2000). Whereas recent analyses suggest that anthracosaurs lie on the amniote stem (Ruta et al. 2003; Ruta and Coates 2007), it is also possible that they fall outside the tetrapod crown-group (Laurin 2000). V'yushkov (1957a, b) distinguished two main lineages of chroniosuchians, the chroniosuchids and the bystrowianids. Whereas chroniosuchids are restricted to the Late Permian of Russia, bystrowianids have been found in Late Permian to Middle Triassic deposits of Russia (Golubev 1998) and have also been reported from the Late Permian of China (Young 1979). Chroniosuchian monophyly is well supported by a number of apomorphies (Novikov and Shishkin 2000). The most important are the sculptured, 'butterfly-shaped' osteoderms that were kinetically connected by an elaborate articulation mechanism and the typical intercentra that possess a unique ball-shaped morphology.

In this study, we describe postcranial remains of a new bystrowianid chroniosuchian from the late Middle Triassic (Lower Keuper, Erfurt Formation) of Kupferzell and the Schumann quarry at Vellberg in southern Germany. The new chroniosuchian taxon resembles most closely the bystrowianid *Synesuchus* and forms the first record of the clade outside Russia and China. At the same time, it

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represents one of the geologically youngest examples of a member of this group.

Institutional abbreviation

Institutional abbreviation includes SMNS for Staatliches Museum für Naturkunde Stuttgart.

Materials

The materials used in this study were SMNS 91034, complete osteoderm fused with tip of neural spine (type); partial osteoderms (SMNS 91036, 91037); and vertebrae (SMNS 81698, 81871 81874, 81876, 81877, 81879).

Localities

Bystrowianid bones were found at two localities in the Lower Keuper: Kupferzell (Bauersbach) and Vellberg (Eschenau), both in Hohenlohe region, northern Baden-Württemberg, Germany.

Results

Systematic palaeontology

1. Chroniosuchia Tatarinov 1972
2. Bystrowianidae V'yushkov 1957a
3. *Bystrowiella* n. g. (honoring eminent Russian palaeontologist A. P. Bystrow for his contributions to vertebrate palaeontology)
4. *Bystrowiella schumanni* n. sp. (named after the Schumann family for their engagement in securing fossils from Lower Keuper)
5. *Type specimen* SMNS 91034 (Figs. 1 and 2)
6. *Type horizon* Untere Graue Mergel, Upper Lower Keuper (Ladinian, upper Middle Triassic) *Type locality* Schumann quarry at Vellberg (Eschenau), Baden-Württemberg, Germany

Diagnosis

Autapomorphies for genus and species: (1) osteoderms laterally more expanded (width to length equals 1, in contrast to 0.7 in *Synesuchus*); (2) in dorsal view, the anterior median incisure is approximately as long as wide and thus proportionally distinctly narrower than in *Synesuchus* with a ratio length to width of 2:3, and articular plate proportionally more slender (osteoderm width to articular plate width: 5.7 in *Bystrowiella* and 3.2 in *Synesuchus*); (3) the lateral edges of the wings are nearly straight in *Bystrowiella*, whereas they are distinctly convex in *Synesuchus*; (5) longitudinal grooves on the articular plate hardly concave and extend anteriorly up to small recess in the lateral side of the ventral process, in contrast to concave grooves in *Synesuchus* terminating at the posterior border of the dorsal plate in two horizontal pits.

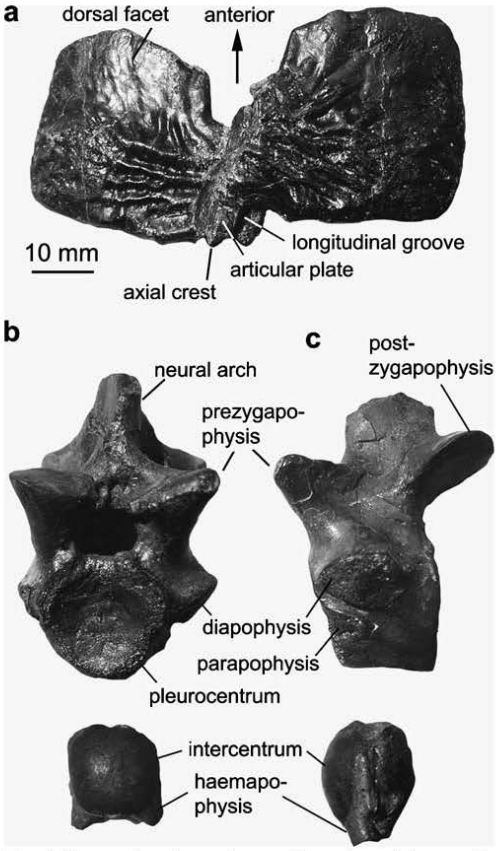

Fig. 1 Photographs of osteoderm and vertebra of *Bystrowiella schumanni* n. g. n. sp. **a** Osteoderm (SMNS 91034) in dorsal view; **b**, **c** vertebra (SMNS 81698). **b** Anterior view; **c** left lateral view

Bystrowiella also shares derived characters with *Synesuchus*: (a) accessory processes are absent; (b) the three posterior processes of the articular plate are not fused, with the medial process being located well above the lateral processes; (c) smooth oblique crests on the ventral surface that terminate anteriorly in the triangular elevation, and (d) ventral depression is comparatively short but deep and has distinct lateral margins.

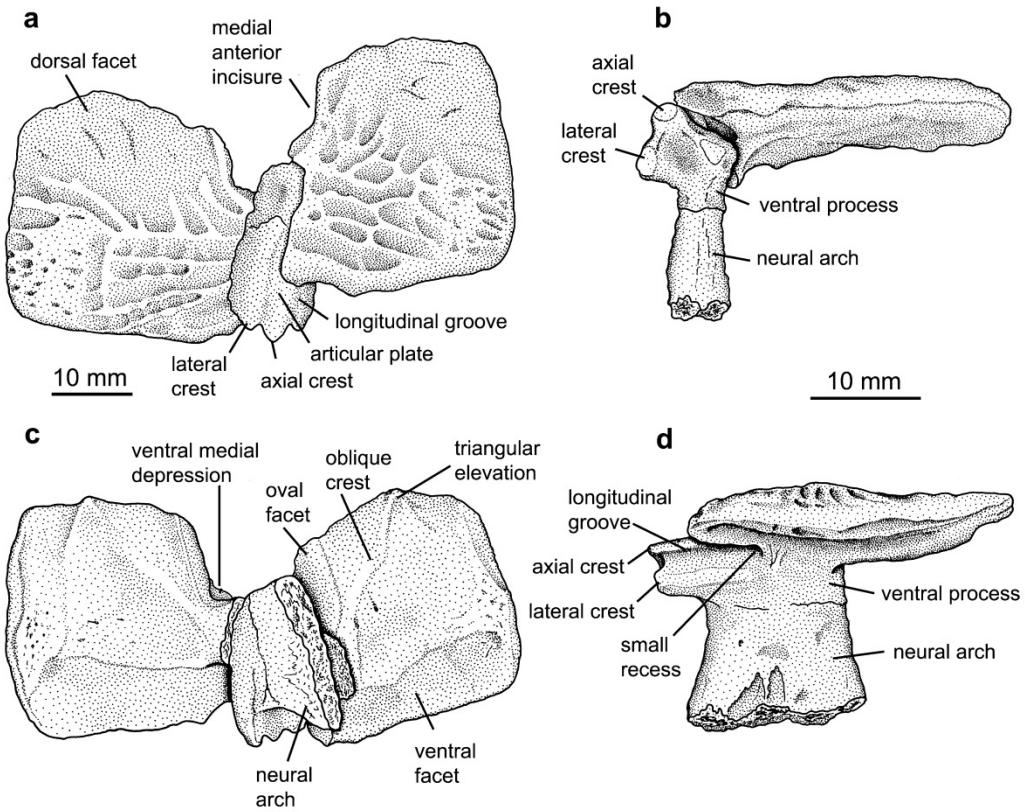

Fig. 2 Osteoderm of *Bystrowiella schumanni* n. g. n. sp. (SMNS 91034). **a** Dorsal view (left wing displaced); **b** posterior view (left wing omitted); **c** ventral view; **d** right lateral view

Description

Osteoderms In this paper, we adopt the terminology of Novikov and Shishkin (2000). The osteoderm (SMNS 91034) consists of a dorsal plate of broad rectangular outline with convex rounded edges, a median articular plate (lamina articularis), and a ventral process (processus ventralis) that was fused to the neural spine (Figs. 1a and 2). The presence of two wings gives the osteoderm the typical butterfly-shaped outline. In contrast to all other bystrowianids except for *Synesuchus* (Novikov and Shishkin 2000), *Bystrowiella* osteoderms have no accessory processes in the median anterior incisure between the wings.

Posterior to the level of the anterior incisure, the dorsal surface is heavily ornamented with sharp ridges that enclose grooves and pits (Figs. 1a and 2a). The median articular plate ends posteriorly in three tapering processes. The median process bears the flat axial crest (crista media) and is located dorsomedially to the lateral processes that bear the lateral crests (cristae laterales) (Fig. 2b). In other bystrowianids, these crests frame two well developed and dorsally conspicuously concave longitudinal grooves (sulci articulares) that terminate at the posterior border of the dorsal, ornamented plate in two horizontal pits (Novikov and Shishkin 2000). These grooves and the pits received the accessory processes of the posteriorly neighboring osteoderm. In contrast, the 'longitudinal grooves' are hardly concave in *Bystrowiella* and reach further anteriorly: they extend beneath the dorsal, sculptured plate and on the lateral face of the ventral process up to a lateral broadening of the latter, where they terminate in a small recess (Fig. 2d). In *Bystrowiella*, the longitudinal grooves receive the oval facets of the anterior incisure (see below) because the accessory processes are absent.

On the ventral surface of the dorsal plate, a well-defined and oval ventromedial facet frames the anterior incisure on either side (Fig. 2c). Posteriorly, it merges into the short

ventral median depression. Immediately posterior to that depression lies the ventral process, which is fused with the tip of the neural spine. The oblique crest runs from the lateral margin of the ventral process towards a triangular elevation at the anterior margin of each wing. From the above-mentioned small recess next to the ventral process, the anterior margin of a shallow, broad ventral facet extends laterally.

Articulation of osteoderms In bystrowianids, the dorsal facets of the anterior portion of each wing underplate the ventral facets of the preceding osteoderm (Novikov and Shishkin 2000). The anterior incisure clasped the median articular plate of the preceding osteoderm. In this arrangement, the prominent oval facets of the posterior osteoderm fit exactly the 'longitudinal grooves' of the next anterior osteoderm. The small recess at the anterior end of the 'longitudinal grooves' received the tip of the oval facets. The median posterior process with the axial crest of the median articular plate was accommodated by the ventral median depression of the posteriorly neighboring osteoderm.

Vertebrae SMNS 81698 from Kupferzell is the best preserved vertebra, consisting of a ball-shaped intercentrum and a massive pleurocentrum fused to the neural arch. The transverse process is short and terminates in an elongate diapophysis (Figs. 1b,c and 3a–c). The prezygapophyses are oriented dorsomedially and slightly anteriorly, whereas the postzygapophyses are oriented ventrolaterally and posteriorly. A round foramen is present ventral to the left prezygapophysis, at the lateral margin of the large neural canal. A corresponding foramen is also present ventral to the right postzygapophysis. Both between the pre- and the postzygapophyses, directly above the neural canal, are located three foramina. Comparison with other bystrowianids (Novikov and Shishkin 2000; Tatarinov 1972) shows that the described foramina represent the openings of the paraneural canals. Only the base of the neural spine is preserved that is slightly shorter than the pleurocentrum.

The cylindrical, deeply amphicoelous pleurocentrum forms the main part of the vertebral centrum and possesses a small notochordal opening. On the anterior portion of the

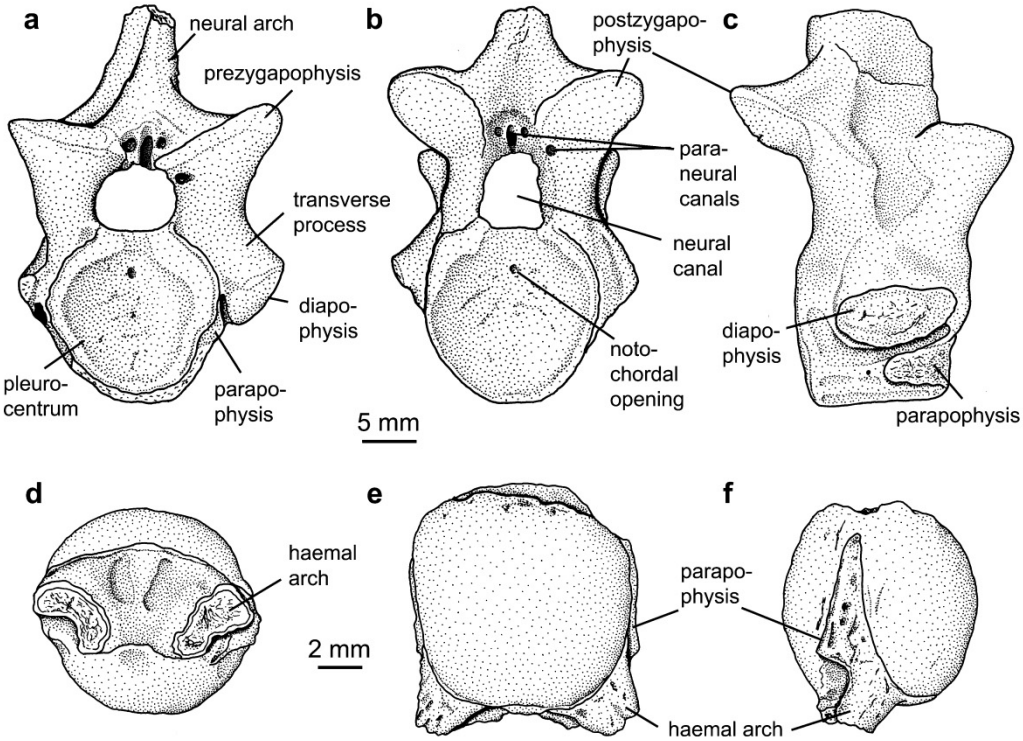

Fig. 3 Vertebra of *Bystrowiella schumanni* n. g. n. sp. (SMNS 81698). **a**–**c** Pleurocentrum with fused neural arch. **a** Anterior view; **b** posterior view; **c** right lateral view. **d**–**f** Intercentrum. **d** Ventral view; **e** anterior view; **f** right lateral view

ventrolateral surface, the parapophysis is visible that is separated from the posterodorsally located diapophysis by an anterodorsally directed, deep incisure (Fig. 3c). The abrupt anterior termination of the parapophysis suggests its continuation on the intercentrum (see below). Two anteroposteriorly directed, broad but low ridges delimit the faintly concave ventral margin of the pleurocentrum, a feature that is also present in other bystrowianids (Novikov and Shishkin 2000).

Associated with SMNS 81698 was a single intercentrum of square-shaped outline in transverse view (Figs. 1b,c and 3d–f). Its anterior and posterior faces are strongly convex, giving it an overall ball-shaped appearance. The ventral surface consists of smooth periosteal bone, is slightly concave, and bears the ventrolateral bases of the hemapophyses (Fig. 3d). In contrast, most parts of the intercentrum are largely coarse and continued by cartilage. The parapophyses are indicated as small swellings. The dorsal surface of the intercentrum is concave and roughened and did not articulate with the neural arch. Therefore, the intercentrum had a free dorsal margin covered by cartilage, which is also reported in the articulated vertebral column of *Chroniosuchus* sp. (V'yushkov 1957b).

SMNS 81698 stems from the anterior tail region, as indicated by the short transverse processes of the neural arch. Trunk vertebrae in bystrowianids have distinctly longer transverse processes (Novikov and Shishkin 2000). Further support for this assumption is given by the hemapophyses on the ventral side of the intercentrum.

Discussion

The discovery of chroniosuchians in Germany greatly extends our knowledge of their geographical range and distribution by Middle Triassic time. It adds to the similarities between the vertebrate faunas of the Eastern European Platform and Central Europe, indicated by the occurrence of the temnospondyl *Mastodonsaurus* in the roughly coeval Lower Keuper and Bukobay Horizon (Shishkin et al. 1995). Only recently reported from Middle Triassic strata at all (Novikov and Shishkin 2000), chroniosuchians were conceived erratic relics of that time. Instead, our findings underline how widespread the group still was in the late Middle Triassic. As chroniosuchians have never been found in the well-collected Buntsandstein or Muschelkalk, the Lower Keuper could reflect the earliest occurrence of this group in Central Europe, and the close resemblance between *Bystrowiella* and *Synesuchus* suggests immigration from the Ural Forelands. However, the absence of chroniosuchians in the Permian and Lower Triassic of Central Europe could alternatively mean a taphonomic overprinting in the way that their habitats are simply not preserved.

In both Russia and Germany, chroniosuchians occupied aquatic environments normally dominated by temnospondyls of broad size range and diverse morphologies (Schoch 2002; Shishkin et al. 1995). It is not clear how they managed to co-exist with the much more numerous temnospondyl taxa, but at least the Kupferzell deposit suggests that while temnospondyls were autochthonous, bones of *Bystrowiella* were washed in from more distant habitats. This indicates that chroniosuchians might have lived in different habitats within the same general area. As the Lower Keuper is known to have formed in diverse swamps and deltas (Schoch 2002), an according differentiation of habitats is likely.

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References

Golubev VK (1998) Narrow-armored chroniosuchians (Amphibia, Anthracosauromorpha) from the Late Permian of Eastern Europe. Paleont J 32:278–287

Gower DJ (1999) The cranial and mandibular osteology of a new rauisuchian archosaur from the Middle Triassic of southern Germany. Stuttgarter Beitr Naturkd B 280:1–49

Ivakhnenko MF, Tverdokhlebova GI (1980) Systematics, morphology and stratigraphic significance of the Upper Permian chroniosuchians from the East of the European part of the USSR. Izdatel'stvo Saratovskogo Universiteta, Saratov (In Russian)

Laurin M (2000) Seymouriamorphs. In: Heatwole H, Carroll RL (eds) Amphibian biology, vol 4, paleontology. Beatty, Chipping, Norton, pp 1064–1080

Novikov IV, Shishkin MA (2000) Triassic chroniosuchians (Amphibia, Anthracosauromorpha) and the evolution of trunk dermal scutes in bystrowianids. Paleont J 34(Suppl 2):165–178

Novikov IV, Shishkin MA, Golubev VK (2000) Permian and Triassic anthracosaurs from Eastern Europe. In: Benton M, Shishkin MA, Unwin D, Kurochkin E (eds) The age of dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge, pp 60–70

Ruta M, Coates MI, Quicke DLJ (2003) Early tetrapod relationships revisited. Biol Rev 78:251–345

Ruta M, Coates MI (2007) Dates, nodes and character conflict: addressing the lissamphibian origin problem. J Syst Palaeont 5:69–122

Schoch RR (1999) Comparative osteology of *Mastodonsaurus giganteus* (Jaeger, 1828) from the Middle Triassic (Lettenkeuper: Longobardian) of Germany (Baden-Württemberg, Bayern, Thüringen). Stuttgarter Beitr Naturkd B 278:1–175

Schoch RR (2002) Stratigraphie und Taphonomie wirbeltierreicher Schichten im Unterkeuper (Mitteltrias) von Vellberg (SW-Deutschland). Stuttgarter Beitr Naturkd B 318:1–30

Schoch RR (2006) A complete trematosaur amphibian from the Middle Triassic of Germany. J Vert Paleont 26:29–43

Shishkin MA, Ochev VG, Tverdokhlebov VP, Vergaj IF, Goman'kov AV, Kalandadze NN, Leonova EM, Lopato AY, Makarova IS, Minikh MG, Molostovskij EM, Novikov IV, Sennikov AG (1995) Biostratigraphy of the Triassic of the Southern Urals. Nauka, Moscow

Tatarinov LP (1972) Seymouriamorphe aus der Fauna der UdSSR. In: Kuhn O (ed) Handbuch der Paläoherpetologie, Part 5B. Gustav Fischer, Stuttgart, pp 70–80

V'yushkov BP (1957a) New kotlassiomorphs from the Tatarian of the European part of the USSR. Trudy Paleont Inst AN SSSR 68:89–107 (In Russian)

V'yushkov BP (1957b) New unusual animals from the Tatarian of the European part of the USSR. Dokl AN SSSR 113:183–186 (In Russian)

Young CC (1979) A new Late Permian fauna from Jiyuan, Honan. Vert Palas 17:99–113 (In Chinese)

Histology and external structure of osteoderms in early tetrapods

Appendix 6

Witzmann, F. & Soler-Gijón, R. 2010. The bone histology of osteoderms in temnospondyl amphibians and in the chroniosuchian *Bystrowiella*. – Acta Zoologica (Stockholm) 91: 96–114.

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The bone histology of osteoderms in temnospondyl amphibians and in the chroniosuchian *Bystrowiella*

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Keywords:
Bone histology, Chroniosuchia, integument, metaplasia, Temnospondyli, osteoderms, Sharpey's fibres

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Abstract

Witzmann, F. and Soler-Gijón, R. 2010. The bone histology of osteoderms in temnospondyl amphibians and in the chroniosuchian *Bystrowiella*. — *Acta Zoologica* (Stockholm) **91**: 96–114

Bone histology of osteoderms in the armoured temnospondyl *Peltobatrachus*, plagiosaurids (*Gerrothorax*, *Plagiosuchus*) and dissorophids (*Aspidosaurus*, *Cacops*, *Platyhystrix*), as well as in the chroniosuchian *Bystrowiella*, is studied. The massive osteoderms of *Peltobatrachus* and *Gerrothorax* consist of homogeneous parallel-fibred bone, whereas in dissorophids, a lightly built, trabecular middle region is mantled by a thin cortex that is composed of a plywood-type structure. In *Bystrowiella* and *Plagiosuchus*, the osteoderms consist to a large degree of interwoven primary fibres and have cell lacunae that bear stumpy canaliculi. The differences in the histological structure of dissorophids and plagiosaurids suggest an iterative evolution of osteoderms. Furthermore, histology in *Plagiosuchus* indicates a metaplastic development of the osteoderms, whereas the osteoderms of *Gerrothorax* represent periosteal ossifications as in dissorophids. This suggests a convergent origin of osteoderms also within plagiosaurids. The extensive armour in *Gerrothorax* probably constituted a calcium reservoir, indicated by cyclical resorption events preserved in the external cortex and interpreted as a physiological response to periodic changes in salinity of the aquatic environment. In contrast, the unique osteoderm structure of dissorophids provides maximum stability and minimum bone mass, and is coherent with the interpretation that the osteoderms served to strengthen the vertebral column during terrestrial locomotion.

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Introduction

Although extant amphibians (anurans, urodeles and gymnophionans) are often characterized by having a naked skin, their dermis has the capability to form ossifications of diverse structure. The cycloid dermal scales of gymnophionans are well known and resemble superficially those of teleosts (Zylberberg *et al.* 1980; Wake and Nygren 1987; Zylberberg and Wake 1990). In the dermis of a variety of anuran taxa, Ruibal and Shoemaker (1984) described externally sculptured bony plates of great structural variability. They referred to these ossifications as osteoderms and compared them to the scales of gymnophionans. In their distinction between dermal scales and osteoderms, Zylberberg and Wake (1990) pointed out that unlike osteoderms, dermal scales are located in pockets in the dermis. Also Castanet *et al.* (2003) emphasized the differing morphological characters between these two types of dermal ossifications: osteoderms are thick plates of bone the external surface of which is sculptured by pits and ridges, whereas dermal scales are usually thinner and are rounded or oval in outline. Apart from dermal scales and osteoderms, a very thin mineralized layer within the dermis, the 'Ground Substance Layer' or 'Eberth–Kastschenko Layer', has been observed in several anuran taxa (Toledo and Jared 1993).

Among fossil temnospondyl amphibians, the presence of ossified dermal scales that cover the trunk, the tail and the limbs is widespread and can be regarded as a plesiomorphic character of tetrapods (Witzmann 2007). Additionally, different lineages of temnospondyls have evolved the possession of

dermal armour consisting of plate-like osteoderms in the postcranial skeleton that vary conspicuously in size, shape and mode of articulation. Broili (1904), Williston (1910), Carroll (1964), DeMar (1966, 1968), Lewis and Vaughn (1965), Bolt (1974), Berman and Lucas (2003), and Dilkes and Brown (2007) described morphology and articulation of the osteoderms covering the neural spines in the Permo-Carboniferous Dissorophidae. Panchen (1959) depicted the covering of the dorsal trunk by osteoderms in *Peltobatrachus*, a Late Permian temnospondyl of uncertain affinities. The osteoderms covering the complete trunk in the Triassic plagiosaurid *Gerrothorax* were described by Nilsson (1946) and Hellrung (2003). Plate-like osteoderms that cover the neural spines are also known in non-temnospondyl basal tetrapods. Their osteoderms have been reported in chroniosuchians (Golubev 1998; Novikov *et al.* 2000; Witzmann *et al.* 2008) and in the seymouriamorph *Kotlassia* (Bystrow 1944). However, the dermal armour that was assigned to this seymouriamorph by Bystrow (1944) was later shown to belong to the chroniosuchian *Chroniosuchus lichareví* (Golubev 2000).

In recent years, the bone histology of osteoderms in fossil and extant reptiles (archosaurs, turtles, placodonts) and of xenarthran mammals has increasingly attracted the interest of zoologists and palaeontologists (e.g. Buffrénil *et al.* 1986; Scheyer and Sander 2004; Hill 2005, 2006; Main *et al.* 2005; Vickaryous and Hall 2006, 2008; Scheyer 2007; Scheyer and Sánchez-Villagra 2007). In spite of the detailed descriptions of temnospondyl osteoderms from morphological (DeMar 1966, 1968; Bolt 1974; Berman and Lucas 2003) and functional (Dilkes and Brown 2007) aspects, the histological structure of osteoderms of temnospondyls or any other group of early tetrapods has never been investigated. Since dermal bones develop within the dermis and are penetrated by several nerves, blood vessels and fibres, their histomorphology in fossil taxa is well suited to derive information concerning the associated soft-parts that are usually not preserved.

The present paper is concerned with the histological structure of plate-like ossifications that can be referred to as osteoderms according to the definition of Castanet *et al.* (2003) in Palaeozoic and Mesozoic temnospondyl amphibians and a Mesozoic chroniosuchian. First, the bone histology of the osteoderms is described in detail. Whether their histology reveals phylogenetic signals, and what can be deduced concerning bone morphogenesis and the structure of the associated soft parts in the living animals is then discussed. Furthermore, what the bone microstructure and histology can tell us concerning functional aspects of the osteoderms and the mode of life of the investigated armoured tetrapods is described.

Materials and Methods

For the present study, postcranial osteoderms for thin-sectioning have been chosen from taxa that represent the major lineages of temnospondyls that are armoured by plate-like osteoderms (dissorophids, plagiosaurids, *Peltobatrachus*). Furthermore, a chroniosuchian was chosen as a representative of armoured, non-temnospondyl basal tetrapods for outgroup comparison.

1 Chroniosuchia: Bystrowianidae. One osteoderm of *Bystrowiella schumanni* from the upper Middle Triassic (Ladinian, Upper Lower Keuper) of Vellberg-Eschenau in southern Germany has been sectioned (SMNS 91226; Figs 1A,B and 2A).
2 *Peltobatrachus pustulatus* UMZC T 270, subsample 35D 101, from the Upper Permian of Tanzania (one osteoderm; Figs 1C,D and 2B).
3 Plagiosauridae. *Gerrothorax* sp. SMNS 83351 from the upper Middle Triassic (Untere Graue Mergel, Ladinian) of Kupferzell-Bauersbach in southern Germany (four dorsal osteoderms; Figs 1E,F and 2C); *Plagiosuchus pustuliferus* SMNS 91227 (one osteoderm; Figs 1G,H and 2D) from the Erfurt Formation, Middle Triassic (Ladinian) of Thuringia. In addition, one articulated postcranial skeleton of *P. pustuliferus* (SMNS 84794) showing a complete series of osteoderms as well as tiny mineralized nodules distributed all over the body was studied morphologically. A sample of the mineralized nodules was studied by scanning electron microscopy (SEM).
4 Dissorophidae. *Aspidosaurus* sp. MCZ 1477 from the Lower Permian of Texas, Rattlesnake Canyon locality, Nocona Formation, USA (three osteoderms; Figs 1I and 2E); *Platyhystrix rugosus* UCMP 33437 from the Lower Permian of New Mexico, Welles Quarry locality, Cutler Formation, USA (one osteoderm; Figs 1J and 2F); *Cacops aspidephorus* UR 2491 from the Lower Permian of Texas, USA (one osteoderm).

The dermal bone fragments were first embedded in synthetic resin (Paraloid B72, an ethyl-methacrylate-copolymer) and then cut sagittally with the exception of the osteoderm of *Platyhystrix*, which was cut horizontally, and the osteoderm of *Plagiosuchus*, from which a transverse section was produced. Thin sections were prepared with a thickness of between 40 and 60 μm using the standard method of Chinsamy and Raath (1992). The thin sections were examined using a Leica DC 300 polarizing stereomicroscope with transmitted ordinary and polarized light. For the investigation of the bone structure by SEM, dermal bone fragments were first cut and polished, and the polished surface was then etched with 10% HCl for 8–10 seconds.

The terminology of Ricqlès *et al.* (1991) and Francillon-Vieillot *et al.* (1990) concerning bone histology will be used throughout the text. Furthermore, we follow Scheyer and Anquetin (2008) in their work on turtle shell bone histology in the use of the term 'external' and 'internal'. An appropriate alternative designation is 'superficial' and 'deep', as used by Hill (2006) instead of 'external' and 'internal', respectively. The external, sculptured surface of the osteoderm faces the

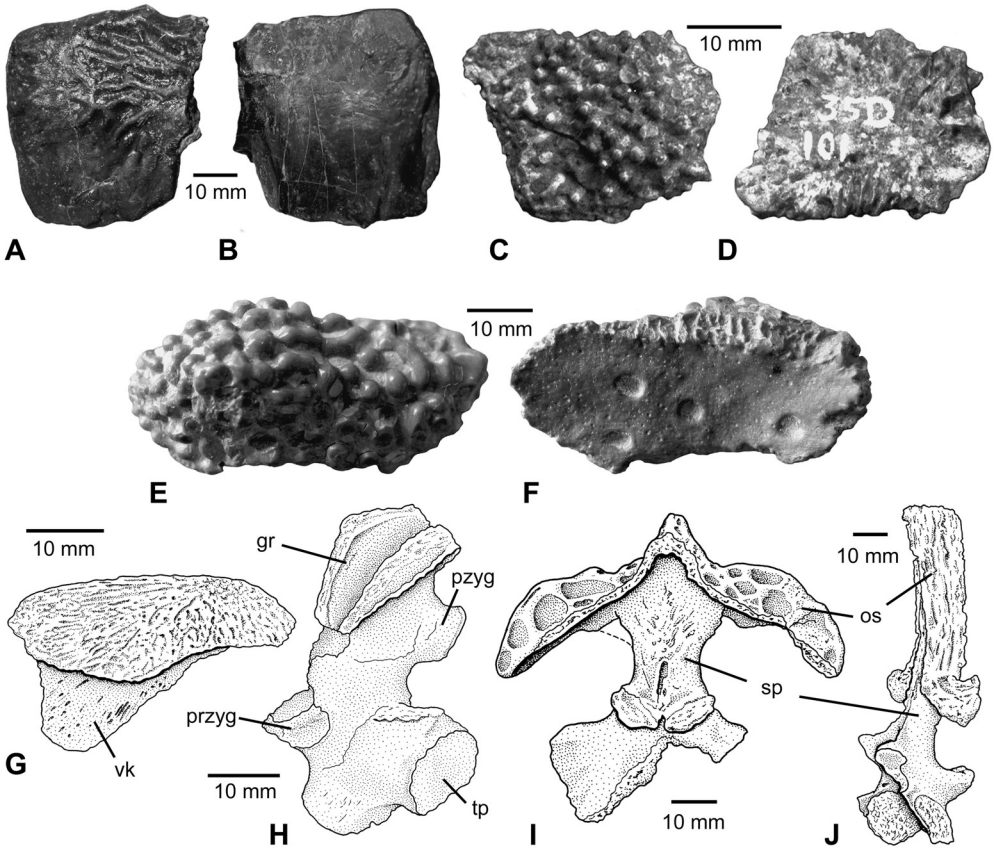

Fig. 1—Osteoderms of basal tetrapods. —**A**, **B**. *Bystrowiella schumanni* (SMNS 91226), external (A) and internal (B) views. —**C**, **D**. *Peltobatrachus pustulatus* (UMZC T 270, subsample 35D 101), external (C) and internal (D) views. —**E**, **F**. *Gerrothorax pustuloglomeratus* (SMNS 83551A), external (E) and internal (F) views. —**G**, **H**. *Plagiosuchus pustuliferus* (SMNS 84794), osteoderm in lateral view (anterior is left) (G), neural arch in lateral view (anterior is left) (H). —**I.** *Aspidosaurus* sp. (MCZ 1477), neural arch and osteoderm in anterior view. —**J**. *Platyhystrix rugosus* (UCMP 33437), neural arch and osteoderm in posterolateral view. gr, groove on neural arch; os, osteoderm; przyg, prezygapophysis; pzyg, postzygapophysis; sp., neural spine; tp, transverse process; vk, ventral keel.

body surface, whereas the internal surface is orientated to the visceral surface of the body. The term 'interior' corresponds to the inner or middle part of an osteoderm. In general, the osteoderms show a diploë structure, i.e. a cancellous or middle region is mantled by compact external and internal cortices. We adopt the terminology 'interwoven structural fibres' (ISF) of Scheyer and Sander (2004), Scheyer and Sánchez-Villagra (2007), Scheyer (2007) and Scheyer and Anquetin (2008) to refer to three-dimensionally interwoven bundles of collagen fibres that show no general isotropy under polarized light in contrast to woven or fibrous bone (Francillon-Vieillot *et al.* 1990; Ricqlès *et al.* 1991), but always exhibit different orientation of the fibres. The sculptural tubercles and ridges on the external surface of the osteoderms are designated as 'saddles' and the grooves between them as 'valleys' in the thin sections.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; MCZ, Museum of Comparative Zoology, Harvard, Cambridge, MA, USA; SMNS, Staatliches Museum für

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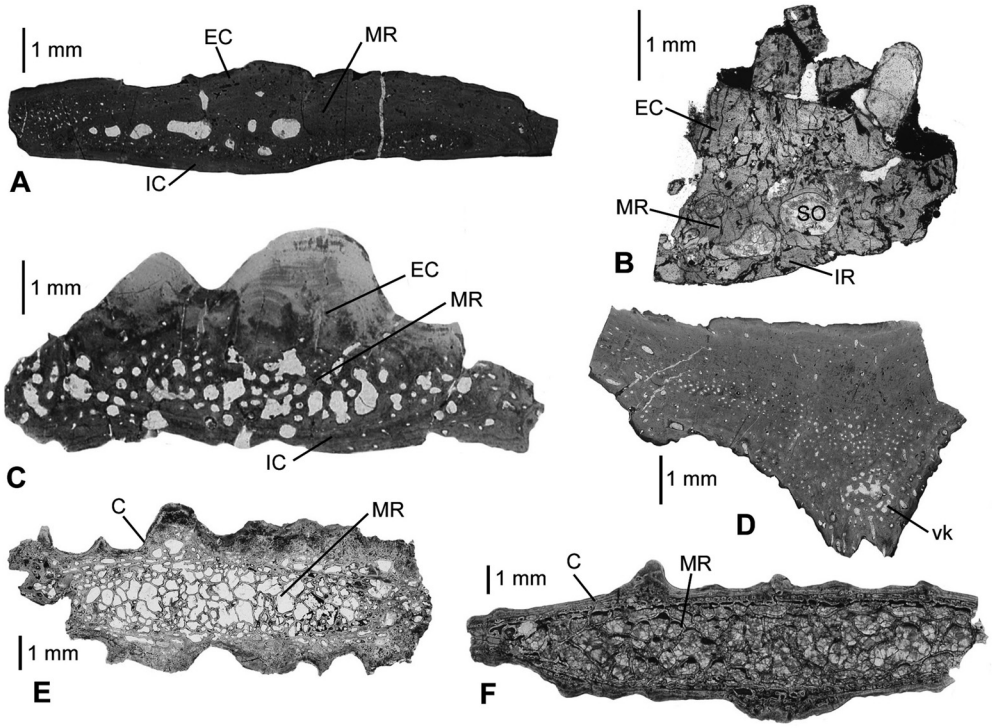

Fig. 2—Overview on histological sections of basal tetrapod osteoderms. —**A**. *Bystrowiella schumanni* (SMNS 91226), sagittal section. —**B**. *Peltobatrachus pustulatus* (UMZC T 270, subsample 35D 101). —**C**. *Gerrothorax pustuloglomeratus* (SMNS 83551A), sagittal section. —**D**. *Plagiosuchus pustuliferus* (SMNS 91227), transverse section. —**E**. *Aspidosaurus* sp. (MCZ 1477), sagittal section. —**F**. *Platyhystrix rugosus* (UCMP), horizontal section. C, cortex; EC, external cortex; IC, internal cortex; MR, middle region; SO, secondary osteon; vk, ventral keel.

Naturkunde, Stuttgart, Germany; UCMP, University of California, Museum of Palaeontology, Berkeley, CA, USA; UMZC University Museum of Zoology, Cambridge, UK; UR, Field Museum of Natural History, Chicago, IL, USA.

Results

Outgroup: bystrowianid chroniosuchians

Chroniosuchians are a group of Late Permian to Middle Triassic tetrapods that are probably nested within the embolomeres among the paraphyletic 'anthracosaurs' (Laurin 2000; Novikov *et al.* 2000). They are characterized by their butterfly-shaped osteoderms that are arranged in a single row on top of the neural spines. Chroniosuchians were probably semi-terrestrial predators (Laurin *et al.* 2004), similar in proportions to extant varanids. Bystrowianid chroniosuchians are known from the Upper Permian of Russia and China, and have been reported from the Middle Triassic of Russia and Germany. In bystrowianids, the osteoderms are fused to the neural spines, and each osteoderm is connected with its anterior and posterior neighbour by an elaborate articulation mechanism (Novikov *et al.* 2000; Witzmann *et al.* 2008).

Bystrowiella schumanni. Typically, the osteoderms of *Bystrowiella* possess two lateral wings ('butterfly shape') that bear externally a reticulate dermal sculpture of ridges and pits, whereas the internal surface is rather smooth (Figs 1A,B and 2A). The lateral wings of each osteoderm underplate the wings of the preceding osteoderm, and the anterior incisure between the wings clasps a posterior process ('median articular plate') of the preceding osteoderm (Witzmann *et al.* 2008). For the present study, one osteoderm of *Bystrowiella* was sectioned.

For thin-sectioning, the left lateral wing of an osteoderm was cut sagittally.

Histology. In *Bystrowiella*, the osteoderm exhibits histologically a diploë structure of rather thin cortices enclosing a large middle region (Figs 2A and 3A). The middle region reaches more than seven times the thickness of the internal and external cortex. The maximum dorsoventral thickness of the osteoderm on the level of the slide is 2.6 mm.

In the external cortex, the sculptural saddles are penetrated by numerous comparatively short, vertical Sharpey's fibres that are fewer in number in the valleys (Fig. 3B). The bone matrix proper of the external cortex is mainly composed of parallel-fibred bone. The bundles of the parallel-fibred bone are better ordered in the sculptural valleys, whereas in the sculptural saddles, they are less well ordered and coarse, and appear in places diffuse under polarized light. This might be because in Sharpey's fibre bone, the intrinsic bone fibres between the Sharpey's fibres are grouped into bundles with changing orientation (Jones and Boyde 1974). Therefore, the parallel-fibred bone may appear often more homogeneous in the valleys than in the saddles. In the more interior parts of the external cortex, the matrix consists to a large degree of a three-dimensional meshwork of ISF in which the bundles of fibres cross each other at about 90°, similar to the middle region (see below). The external cortex is moderately vascularized by primary vascular canals that may anastomose; the externalmost part, however, is avascular. Scattered secondary osteons are visible more internally. The bone cell lacunae in the parallel-fibred bone are mostly round with canaliculi of varying length, whereas the lacunae are irregular in shape in ISF. Growth marks are weakly developed and follow the external sculpture. The 'buried' external sculpture of a former generation is visible in the bone matrix.

In the middle region, the primary bone matrix is homogeneously composed of ISF that form a three-dimensional meshwork of strong fibre bundles (Fig. 3C–E). Under polarized light, the birefringence patterns of the collagen fibres are clearly visible. Fibre bundles that are orientated perpendicular to the plane of section have a globular appearance under normal transmitted light (Fig. 3F). Focusing on different planes of the slide under the microscope shows that these structures do not represent real globules, like cell spaces for instance, but fibres that extend perpendicularly or obliquely to the image plane. Between the fibres, bone cell lacunae of irregular, often star-shaped outline with short or no canaliculi are present. Primary osteons and primary vascular canals populate the bone, and also some secondary osteons in which the Haversian canals can be quite large are present (Fig. 3A,C).

The internal cortex has about half the thickness of the external cortex and consists of coarse parallel-fibred bone. Vascularization consists of very few primary vascular canals aligned approximately parallel to the internal bone surface, and Sharpey's fibres cannot be detected (Fig. 3G).

Temnospondyli incertae sedis: Peltobatrachus pustulatus

Peltobatrachus pustulatus from Tanzania is a Late Permian temnospondyl with a presumed terrestrial mode of life (Panchen 1959; Hellrung 2003), whose phylogenetic relationships are still a matter of debate. Panchen (1959) postulated a close relationship of *Peltobatrachus* with the Triassic plagiosaurids. Also Milner (1990) regarded *Peltobatrachus* and plagiosaurids as sister-groups, and placed them together as sister-group to the Dissorophoidea and lissamphibians. In contrast, the phylogenetic analysis of Yates and Warren (2000) found *Peltobatrachus* to be a basal stereospondyl, and the plagiosaurids to be 'higher' stereospondyls and the sister group to *Laidleria*. Also Hellrung (2003) argued against a close relationship between *Peltobatrachus* and plagiosaurids.

General morphology. The morphology and arrangement of the dermal armour of *Peltobatrachus* was described in detail by Panchen (1959). The armour consists of bands of osteoderms between a pectoral and pelvic shield composed of firmly sutured osteoderms. Also the anterior tail is covered by osteoderms. The bands themselves were rigid and their osteoderms connected by interdigitating sutures. Each band articulated to the anteriorly and posteriorly neighbouring bands by overlapping sutures that probably permitted a certain degree of flexibility between the successive bands. The armour of *Peltobatrachus* covered only the dorsal parts of trunk and anterior tail, whereas a ventral counterpart was obviously not developed. The bands of osteoderms can be divided in neural and costal series. At their anterior and posterior margins, the median neurals possess ventral

Fig. 3—Thin sections of basal tetrapod osteoderms. —**A–G**. *Bystrowiella schumanni* (SMNS 91226). —**A**. Histological overview showing thin external and internal cortices and a large middle region in normal transmitted light. —**B**. External cortex in polarized light with Sharpey's fibres in the sculptural saddle; the bone tissue consists of parallel-fibred bone and more interiorly of interwoven structural fibres (ISF); primary vascular canals penetrate the bone. —**C**. Middle region showing primary bone tissue that is composed of ISF; secondary osteons with lamellar bone are visible. —**D, E**. Close up of the ISF of the middle region in polarized light. —**F**. ISF of middle region in normal transmitted light, transversely cut fibres appear 'globular' with bone cell lacunae in between. —**G**. Internal cortex with parts of the middle region, the internal cortex is poorly vascularized and consists of parallel-fibred bone, normal transmitted light. —**H**. *Peltobatrachus pustulatus* (UMZC T 270, subsample 35D 101). External cortex and columnar tubercles consisting of parallel-fibred bone. Normal transmitted light. cl, bone cell lacuna; CT, columnar tubercle; EC, external cortex; ft, transversely cut intrinsic fibres; IC, internal cortex; ISF, interwoven structural fibres; LB, lamellar bone; MR, middle region; PFB, parallel-fibred bone; PVC, primary vascular canals; ShF, Sharpey's fibres; SO, secondary osteon.

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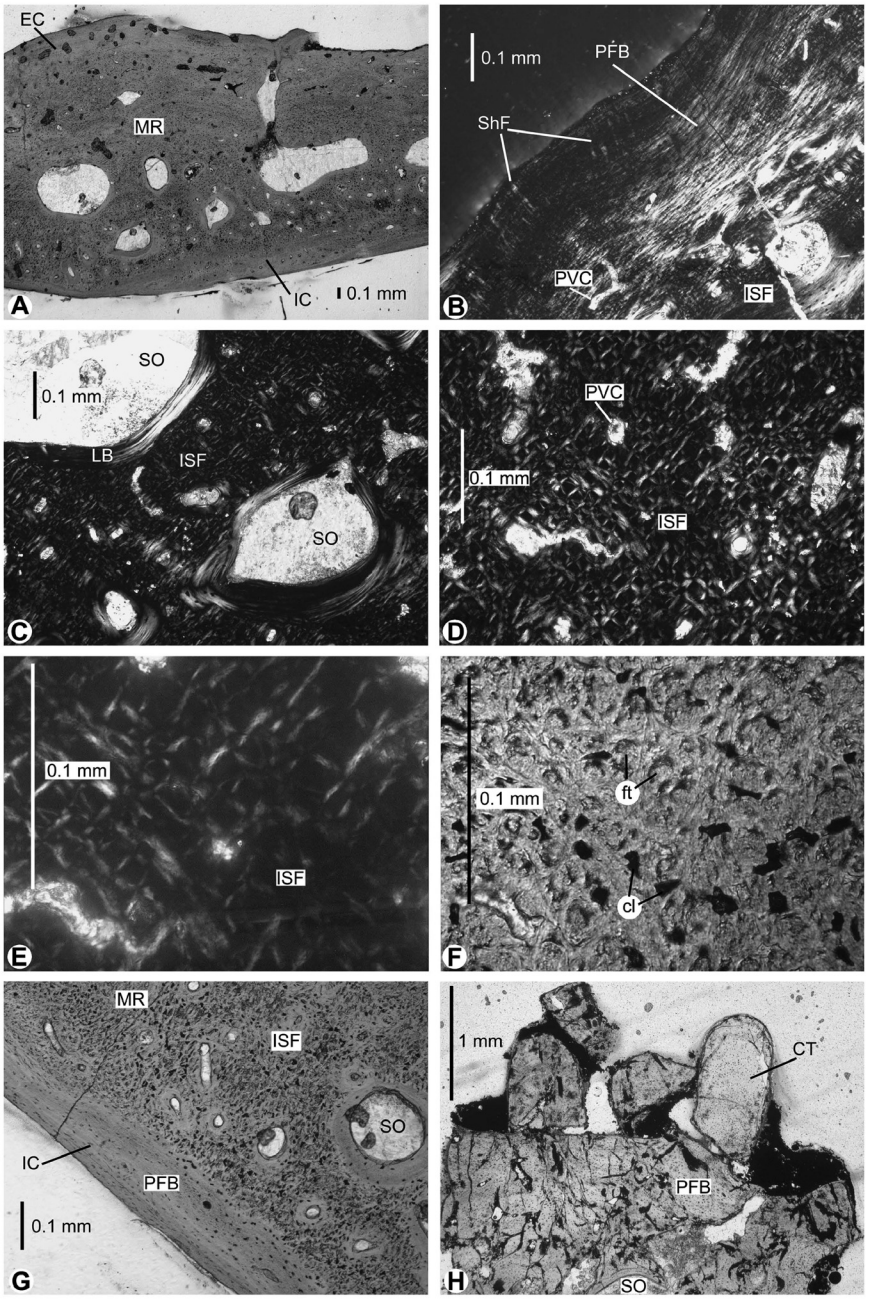
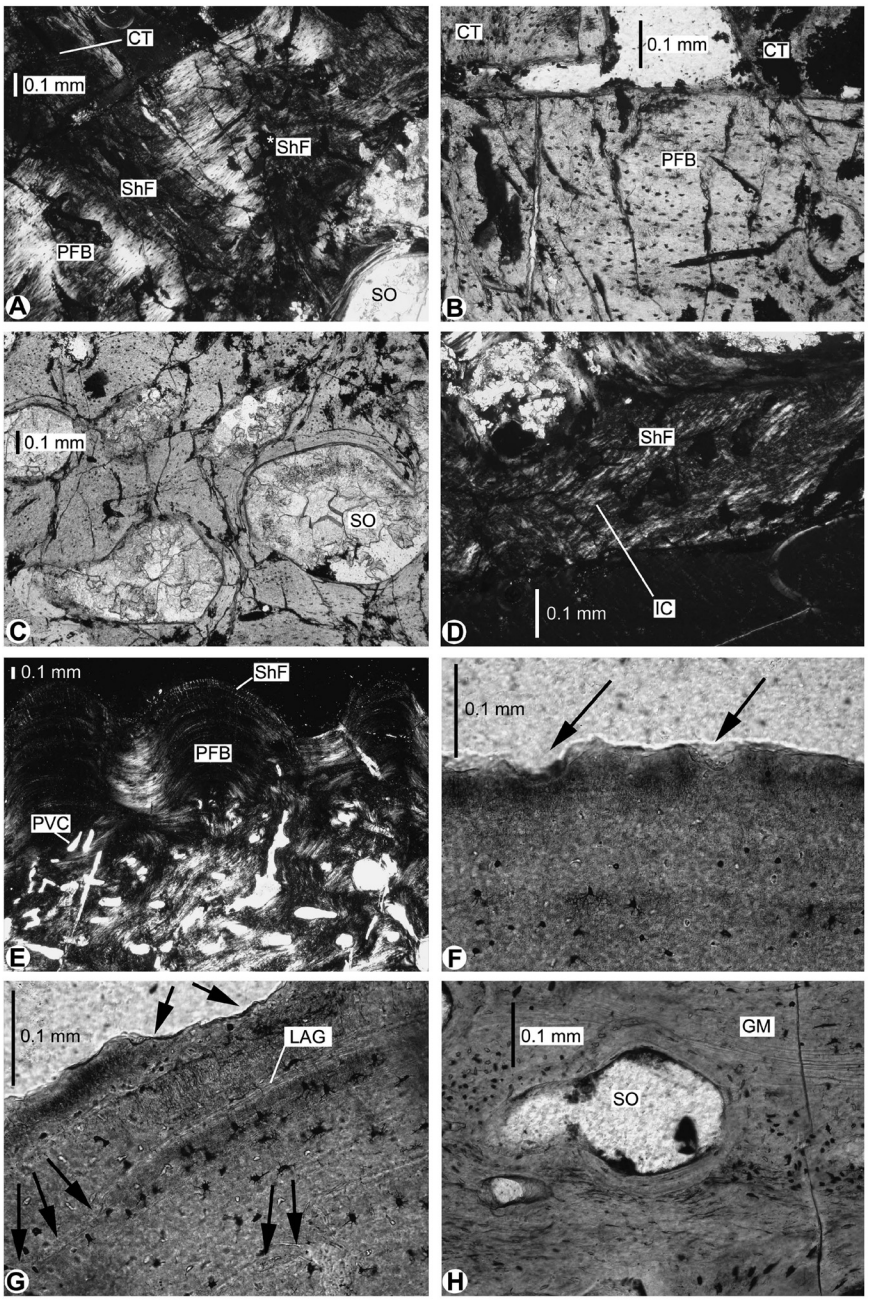




depressions that received the neural spines of two successive vertebrae, and no co-ossification between spines and osteoderms took place.

One osteoderm of *Peltobatrachus*, UMZC T 270, subsample 35D 101, was sectioned for the present study (Figs 1C,D and 2B). As a result of its small size, this specimen is probably a caudal osteoderm. It is roughly trapezoidal in outline and bears a distinct pustular sculpture on its external (dorsal) surface that is convex with a median elevation that might represent the centre of ossification. The internal (ventral) surface is slightly concave. It is unsculptured, but bears irregular crests and depressions distally. One margin, that bears several ridges, probably overlapped a neighbouring osteoderm.

Histology. The osteoderm possesses a diploë structure with a thick external cortex that bears high, columnar tubercles (Fig. 2B). The middle, coarse cancellous region and the internal cortex are comparatively thin, whereas the middle region is more than twice as thick as the internal cortex.

The thickness of the external cortex (without tubercles) exceeds that of the middle region plus the internal cortex. The columnar sculptural tubercles are unusually high, and the sculptural valleys are rather plane (Fig. 3H). This morphology resembles surprisingly closely the outer cortex of the shell of the turtle *Naomichelys* (Scheyer and Anquetin 2008). The bone matrix is composed of homogeneous layers of parallel-fibred bone (Fig. 4A). Except for the tubercles, which are avascular, the external cortex is vascularized by several anastomosing primary vascular canals and primary osteons. The bone cell lacunae are mostly round in the tubercles and slightly flattened in the sculptural valleys (Fig. 4B). Some lacunae lack canaliculi, in others, they are long and branching. The presence of Sharpey's fibres is restricted to the sculptural tubercles where they are rather irregularly arranged. They are moderately thick and long, some extending until to the middle region. Growth marks are present, but indistinct and difficult to trace. A 'buried' tubercle of an earlier generation – still with Sharpey's fibres – is visible within the external cortex (Fig. 4A).

The thin middle region is coarse cancellous bone and bears several secondary osteons that have mostly large Haversian canals (Fig. 4C). The primary bone matrix is composed of fine and in parts more coarse parallel-fibred bone.

In the internal cortex, fine to coarse parallel-fibred bone constitutes the matrix and the bone cell lacunae are most often spindular with moderately long canaliculi. Sharpey's fibres, whose outline is often less well defined, penetrate the internal cortex at an angle of approximately 40° (Fig. 4D).

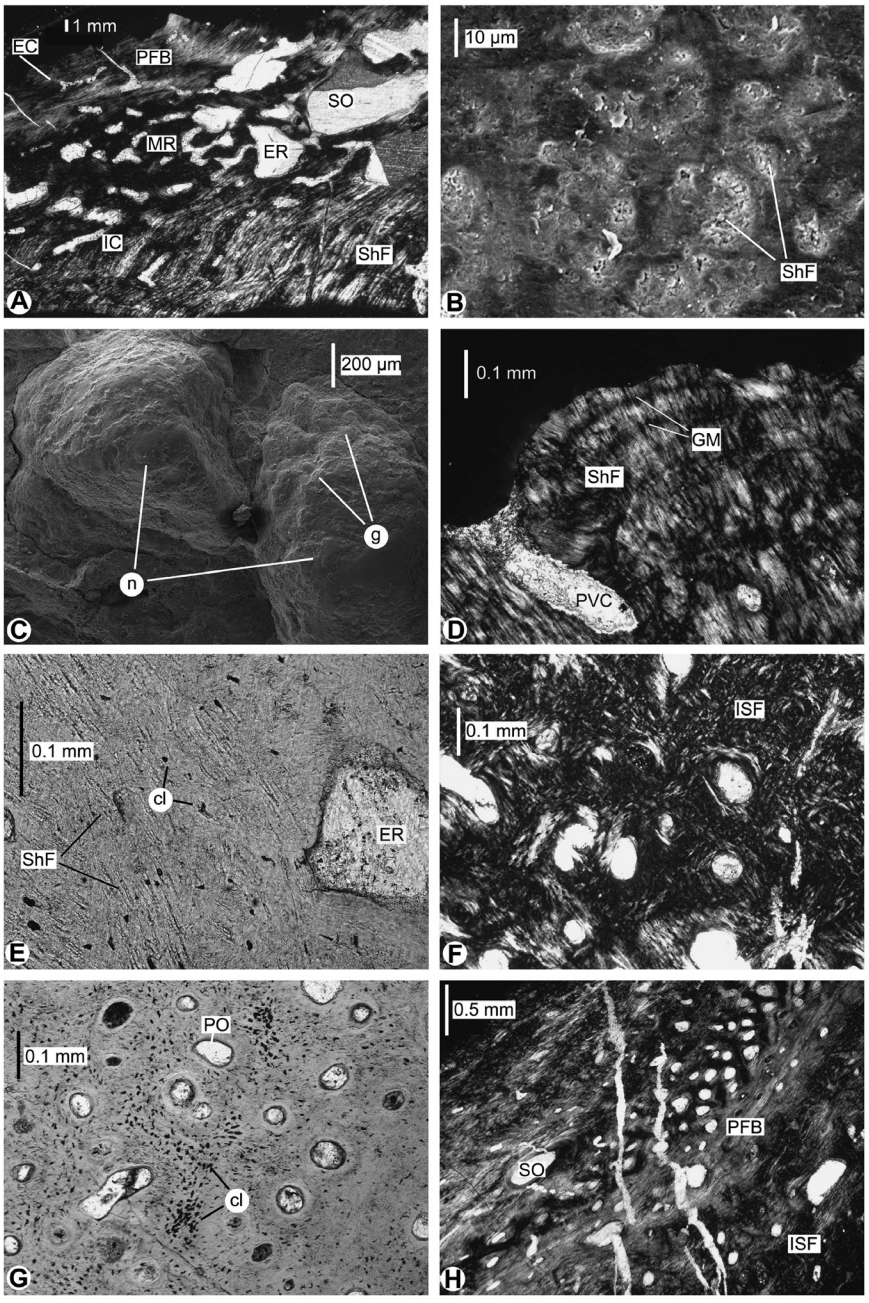
Temnospondyli: Plagiosauridae

Plagiosaurids are a group of Early to Late Triassic, perennibranchiate temnospondyls that are often heavily armoured with osteoderms. They are considered to be bottom-dwelling ambush predators in freshwater and brackish environments (DeFauw 1989; Warren 2000; Hellrung 2003).

Gerrothorax pustuloglomeratus. This plagiosaurid was completely armoured by osteoderms on the dorsal and ventral sides of the trunk (Nilsson 1946; Hellrung 2003). On the dorsal side of the trunk, the osteoderms are of different size, rhombic to polygonal in shape, and their margins are very variable, from straight or curved to serrated. The osteoderms that directly overlaid the top of the neural spines are more quadrangular to rectangular. They were not co-ossified with the spines and overlap in the form of a shingled roof anteroposteriorly (Nilsson 1946). The ventral armour consists of polygonal plates whose longitudinal axes are directed anteromedially; therefore, the ventral osteoderms are arranged in an inverted V-pattern corresponding to the gastral scales ('gastral ribs') that are positioned on the internal (dorsal) side of the osteoderms.

From *Gerrothorax pustuloglomeratus*, six osteoderms (SMNS 83351, 83361) were sectioned for the present study. The rectangular osteoderms are derived from the median series that overlaid the neural spines, and the more elongate ones are from the lateral to the median series. Their external surface is dorsally convex and possesses a pustular dermal sculpture of tubercles that are sometimes connected by low ridges (Fig. 1E). The region of overlap with the anteriorly and posteriorly neighboured osteoderm, respectively, is a short shelf with longitudinal striae on the anterodorsal and

Fig. 4—Thin sections of basal tetrapod osteoderms. —**A–D**. *Peltobatrachus pustulatus* (UMZC T 270, subsample 35D 101). —**A**. External cortex in polarized light composed of parallel-fibred bone with Sharpey's fibres in the columnar tubercles; a 'buried' columnar tubercle with Sharpey's fibres is visible in the cortex and marked with an asterisk (*). —**B**. External cortex with bone cell lacunae in normal transmitted light. —**C**. Middle region with secondary osteons in normal transmitted light. —**D**. Internal cortex in polarized light, penetrated by oblique Sharpey's fibres. —**E–H**. *Gerrothorax pustuloglomeratus*. —**E**. External cortex and middle region of SMNS 84768 in polarized light; the external cortex consists of parallel-fibred bone, and Sharpey's fibres are visible in the sculptural saddles; the middle region bears several primary vascular canals and erosion rooms. —**F**. External bone surface of SMNS 83351 with alveolar structures (arrows) indicating resorption of bone, normal transmitted light. —**G**. External cortex of SMNS 83351 showing trough-like resorptive structures on the bone surface and within the cortex (arrows) in normal light; the troughs are associated with lines of arrested growth. —**H**. Middle region of SMNS 83351 in normal transmitted light with secondary osteon and growth marks. CT, columnar tubercle; EC, external cortex; ER, erosion room; GM, growth marks; IC, internal cortex; ISF, interwoven structural fibres; LAG, line of arrested growth; MR, middle region; PFB, parallel-fibred bone; PVC, primary vascular canals; ShF, Sharpey's fibres; SO, secondary osteon.



on the posteroventral surfaces (Fig. 1F). The internal (ventral) surface of the osteoderms is concave and smooth with the exception of some (mostly 4–10) round pits measuring 2–4 mm in cross-section (Fig. 1F).

Histology. The thin sections reveal that the osteoderms possess a diploë structure with a rather thick compact external cortex whose thickness (without tubercles) measures twice the thickness of the internal cortex; the middle region is more than twice as thick as the internal cortex (Fig. 2C).

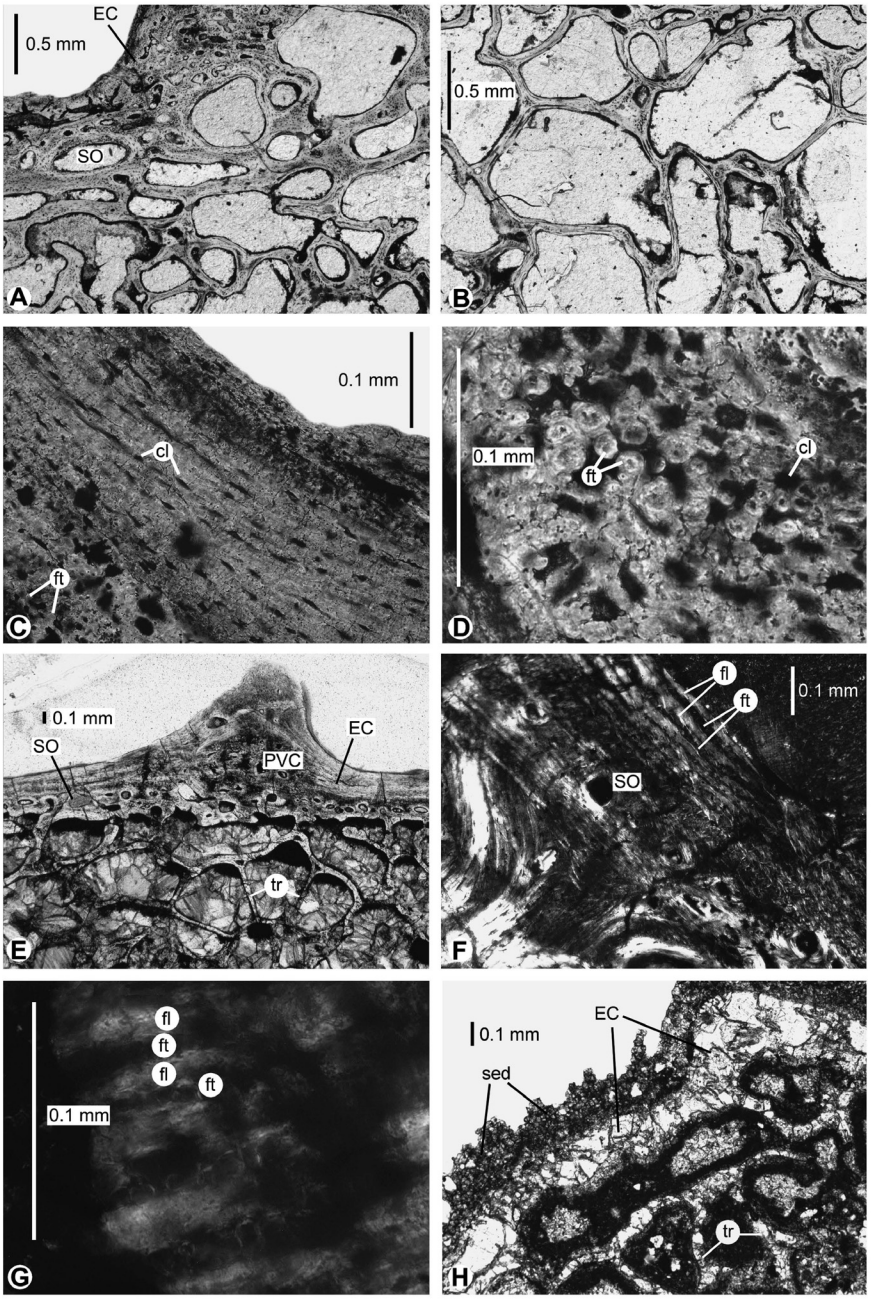
In the outer part of the external cortex, numerous, often S-shaped bundles of Sharpey's fibres are present (Fig. 4E). In the sculptural saddles, the number and density of Sharpey's fibres is normally larger than in the valleys. The fibres are thinner and shorter than those in the internal cortex (see below). The bone matrix of the external cortex consists to a large degree of parallel-fibred bone with numerous cyclical growth marks that run parallel to the sculptured bone surface. Within the sculptural saddles, the parallel-fibred bone remains sometimes diffuse dark under polarized light, probably because of the superposition of the Sharpey's fibres and the less ordered, more randomly arranged intrinsic bone fibres in Sharpey's fibre bone, and associated with this is a rounder outline of the bone cell lacunae (Jones and Boyde 1974). The lacunae, in contrast, are long-oval and have often long, branching canaliculi in the parallel-fibred bone of the sculptural valleys in which the Sharpey's fibres are mostly scarce. Frequently, 'buried' sculptural saddles of earlier generations are observable, in parts still with fan-shaped Sharpey's fibres. Anastomosing, simple primary vascular canals are visible, and isolated primary osteons and young secondary osteons with large Haversian canals may be present in the interior part of the external cortex. Cyclical resorption events producing trough or alveolar-like patterns are preserved within the external cortex and on the bone surface, and are associated with growth marks, i.e. a temporary slowing down or cessation of bone growth (Fig. 4F,G).

The middle region is often trabecular and extensively remodelled: several secondary osteons form clusters and may constitute Haversian tissue. Some osteons bear extensive vascular spaces, and numerous large erosion cavities without a lining of secondary lamellar bone are present. In places, the cavities are smaller, secondary osteons (Fig. 4H) are fewer in number, and primary osteons become more numerous. The bone can be designated here as coarse cancellous. The primary bone tissue is parallel-fibred. Vestiges of the Sharpey's fibres of the internal cortex (see below) are visible in the primary bone matrix in places. In direction to the internal cortex, the middle region becomes increasingly compact, but is nevertheless well vascularized by interconnected primary vascular canals.

The internal cortex consists of parallel fibred bone that is not well ordered, i.e. the bone fibres vary in their orientation. Strong, densely arranged bundles of Sharpey's fibres extend into the internal cortex at an oblique angle (Fig. 5A). The Sharpey's fibres are much longer and broader than those of the external cortex and extend to the middle region. The bundles are mostly subparallel to each other but may interweave in some regions. In specimen SMNS 83351 (3), the Sharpey's fibres converge towards the centre of the osteoderm. The same specimen shows that the Sharpey's fibres are partially interwoven with the fibre bundles of the parallel-fibred bone. Except for the region immediately close to the internal surface of the osteoderm, scattered vascular spaces and primary vascular canals are present and are partially arranged in rows parallel to the internal bone surface. An SEM of the horizontally etched internal surface of the osteoderms shows the Sharpey's fibre bundles in cross-section (Fig. 5B). Their shape is oval to round (depending on their angle of penetration), and they are of varying size. In contrast to the bone matrix proper, the cross-sectioned fibre bundles possess several slits and holes, indicating that the fibre bundles were less mineralized than the surrounding bone matrix.

Plagiosuchus pustuliferus. In *Plagiosuchus*, the entire trunk was not covered with plate-like osteoderms as in *Gerrothorax*, but a single row of osteoderms was situated on top of the neural spines. The osteoderms are rounded quadrangular in outline (Fig. 1G). In the anterior trunk region, they are slightly wider than long and narrow anteriorly. From anterior to posterior in the vertebral column, the osteoderms become increasingly narrower, so that the osteoderms of the posterior part of the trunk are almost twice as long as wide. Their dorsal (external) surface is rather plane with an elevation in the posterior region; in the posterior part of the trunk, they

Fig. 5—Dermal ossifications of basal tetrapods. —**A, B**. *Gerrothorax pustuloglomeratus* (SMNS 83351b). —**A**. Overview of SMNS 83351b in polarized light with the external cortex being partially eroded; note the strong bundles of Sharpey's fibres penetrating the internal cortex. —**B**. SEM of etched surface of the internal region of SMNS 83351b; the transversely or obliquely cut Sharpey's fibres are round to oval and brighter and more porous than the bone matrix proper. —**C–H**. *Plagiosuchus pustuliferus* (SMNS 84794). —**C**. SEM of mineralized nodules that are preserved external to the osteoderms and the ventral gastral scales, and are composed of tiny globules. —**D**. External cortex with dense Sharpey's fibres and growth marks in polarized light. —**E**. External cortex with Sharpey's fibres, cell lacunae and an erosion room in normal transmitted light. —**F**. Middle region of proximal portion of osteoderm in polarized light; the primary matrix consists of interwoven structural fibres (ISF), vascularized mainly by simple primary canals and primary osteons. —**G**. Bone cell lacunae in the ISF appear in local clusters in the middle region, normal transmitted light. —**H**. More distal portion of the middle region, that is here composed of parallel-fibred bone with transitions to ISF. Polarized light. cl, bone cell lacuna; ER, erosion room; g, globules; GM, growth marks; ISF, interwoven structural fibres; n, mineralized nodules; PFB, parallel-fibred bone; ShF, Sharpey's fibres; SO, secondary osteon.



become slightly more convex. The osteoderm surface bears no dermal sculpture of pits and ridges or tubercles as is common in the dermal bones of other temnospondyls. Rather, the surface is roughened and appears spongy, with tiny grooves radiating outward from the posterior elevation. The anterior region of each osteoderm was slightly (not more than one-seventh of the osteoderm length) overlapped by the posterior part of the anteriorly located osteoderm. The osteoderms were not co-ossified with the neural spines but articulated via a ventral, sagittally aligned keel with the neural arches (Fig. 1G). In its dorsal part, the keel is almost as long as the dorsal plate of the osteoderm. It tapers ventrally to a blunt apex, with the anterior edge of the keel being almost vertically aligned, whereas the posterior edge forms an angle of approximately 45° with the plate of the osteoderm. The posteroventral edge of the keel is accommodated by a groove on the anterodorsal portion of the neural spine (Fig. 1H).

Mineralized nodules. On the external surface of the osteoderms, tiny mineralized nodules of different size (mostly ranging from 0.3 mm to more than 1 mm) and shape can be found. The SEM reveals that each nodule consists of several small globules (Fig. 5C). The mineralized nodules are also present external (ventral) to the spindular gastral scales of the belly, and are visible both on and between the ribs throughout the trunk and in the anterior part of the tail, on the dorsal surface of the interclavicle, and in the hindlimb (the forelimb is not preserved) between tibia and fibula, but not in the pes.

Histology. For histological studies, one osteoderm of the anterior trunk region was sectioned transversely to the sagittal axis of the animal. In contrast to *Gerrothorax*, the osteoderm shows no diploë structure (Fig. 2D). A thin, rather compact middle region is populated by primary vascular canals, primary osteons, and a few secondary osteons. It is framed by thick, poorly vascularized external and internal regions. The boundaries between the middle region and the external and internal regions follow approximately the course of the ventral keel (i.e. the three regions are roughly triangular with the apex directed ventrally).

In the external region, the bone matrix proper is often obscured by extensively developed and very densely arranged, long Sharpey's fibres (Fig. 5D,E). In some regions, however, it is visible that the bone matrix consists of ISF bundles. In the lateral portion of the osteoderm, the majority of the Sharpey's fibres are orientated medioventrally and appear as a shallow 'S'. Towards the proximal portion of the osteoderm, i.e. the region dorsal to the ventral keel, the angle of the Sharpey's fibres becomes increasingly steeper and is approximately perpendicular to the external bone surface in the region directly above the keel. In spite of this general direction, the angle between the individual Sharpey's fibres may vary locally, so that they may interweave. Growth marks are visible in the external part of the external region. The vascularization of the external region is rather poor and consists mostly of primary vascular canals and to a lesser degree of primary osteons. The bone cell lacunae are less abundant than in the middle region (see below) and are mostly round and lack canaliculi (Fig. 5E).

The middle region is thin compared to the internal and external regions. Primary vascular canals are much more numerous than secondary osteons, and because the canals are small in diameter, the bone appears rather compact. Little secondary remodelling took place. Towards the proximal part of the osteoderm (above the keel), the matrix of the middle region consists mainly of ISF (Fig. 5F). Bone cell lacunae in the ISF appear unordered in local clusters (Fig. 5G). They are of irregular shape and mostly lack canaliculi. In the lateral part of the osteoderm, the bone matrix consists mostly of homogeneous parallel-fibred bone (Fig. 5H).

The internal region and especially the conspicuous ventral keel that articulated with the neural spine, is vascularized by several simple primary canals and scattered primary osteons. Apart from the ventral keel, the internal surface bears shallow ridges. The ventral part of the keel is penetrated by densely arranged, thick bundles of Sharpey's fibres that extend in a dorsoventral direction. Also dorsoventrally arranged simple primary canals are visible in the keel, sometimes opening to the ventral surface (Fig. 2D). The bone matrix is composed of ISF, through which the fibre bundles course in an irregular fashion. Sharpey's fibres are also visible at the ventrolateral margins of the keel, directed also dorsoventrally, but they are not as long and dense as in the ventral part of the keel. The internal region of the plate-like extensions dorsolateral to the keel is less well vascularized by simple primary canals and primary osteons, but they are larger in number than in the external region. Sharpey's fibres are not as dense as in the keel, although they are quite long. They are most numerous in the shallow ventral ridges. Most of the Sharpey's fibres are arranged obliquely in a dorsolateral

Fig. 6—Thin sections of dissorophid osteoderms. —**A–D**. *Aspidosaurus* sp. (MCZ 1477). —**A**. External cortex and trabecular middle region. —**B**. Gracile trabeculae of the middle region. —**C**. External cortex in normal transmitted light, with spindular bone cell lacunae visible in longitudinally cut bone fibres, and transversely cut bone fibres in the lower left corner. —**D**. External cortex in normal transmitted light, close up of transversely cut bone fibres with star-shaped bone cell lacunae in between. —**E–G**. *Platyhystrix rugosus* (UCMP). —**E**. External cortex and trabecular middle region in normal transmitted light. —**F**. External cortex in polarized light showing a plywood-like tissue externally. —**G**. Close up of plywood-like tissue of the external cortex in polarized light; note the fine meshwork that delineates the transversely cut fibres. —**H**. *Cacops aspidephorus* (UR 2491), external cortex and trabecular middle region. Recrystallization makes it impossible to determine the types of bone tissue. cl, bone cell lacuna; EC, external cortex; ER, erosion room; fl, longitudinally cut intrinsic fibre; ft, transversely cut intrinsic fibre; PVC, primary vascular canals; SO, secondary osteon.

direction. Throughout the internal region, the bone matrix consists of ISF, as in the keel. Cyclical growth marks are visible in some regions, but they are weakly developed and have a diffuse appearance.

Temnospondyli: Dissorophidae

The small to medium-sized representatives of the Dissorophoidea comprise the most terrestrial temnospondyls. The group is of great importance because it gave rise to some or all extant groups of lissamphibians (Schoch and Milner 2004; Ruta and Coates 2007; Anderson *et al.* 2008), although this hypothesis has been disputed by some authors (e.g. Vallin and Laurin 2004; references therein). In the Dissorophoidea, osteoderm-bearing taxa are found among the Dissorophidae. The occurrence of their representatives is known from the Late Pennsylvanian to the Late Permian, and they were widely distributed from North America to Western and Central Europe, Russia and China (Gubin 1980; Li and Cheng 1999; Berman and Lucas 2003; Witzmann 2005). The osteoderms of dissorophids are aligned along the vertebral column on top of the neural spines in a single row, whereby one or two osteoderms per vertebral segment may occur. DeMar (1966) distinguished two morphological groups of osteoderms in dissorophids. Those of the Dissorophinae are not fused with the neural arches; instead, the neural arches generally possess grooves that articulate with the ventral processes of the osteoderms (DeMar 1966; Dilkes and Brown 2007). In the Aspidosaurinae, in contrast, the neural spines broaden in their dorsal portion and and co-ossify firmly with the osteoderms (Fig. 1I,J). *Platyhystrix*, *Aspidosaurus* and *Cacops*, whose osteoderms were investigated for this study, belong to the Aspidosaurinae.

Aspidosaurus sp. The osteoderms bear a roof-shaped outline in anterior and posterior view, respectively (Fig. 1I). Each half of the roof descends gently in a ventrolateral direction from a moderately high sagittal crest. The external surface bears a coarse sculpture consisting of high crests with tubercles, surrounding large oval pits. Both the dorsal and ventral surfaces of the lateral halves are sculptured. For processing the thin sections, the lateral halves of the osteoderms were cut in sagittal plane. These lateral halves are quite thick (up to 10 mm). The general morphology of *Aspidosaurus* is basically similar to that of *Platyhystrix* (see below), but with the difference that osteoderms and neural arches are less extended in height, the lateral halves project further laterally, and the sculpture of ridges and pits is much more pronounced.

Histology. The thin sections reveal that the greatest portion of the osteoderm consists of highly porous trabecular bone with extensive vascular spaces, and is mantled by a thin, compact external cortex (Figs 2E and 6A,B). The interior part of the cortex bears numerous secondary osteons, and the external part is well vascularized mostly by simple primary canals.

In its externalmost portion, the external cortex consists of homogeneous parallel-fibred bone in the sculptural valleys and in the flanks of the sculptural saddles. More interiorly in the cortex, the orientation of the bone fibres changes: portions of longitudinally cut parallel fibred bone alternate with those in which the fibres are cut approximately transversely. The shape of the canaliculi-bearing bone cell lacunae is long-oval in those regions were the bone fibres are cut longitudinally (Fig. 6C); in contrast, they are round to star-shaped in those parts where the bone fibres are cut approximately transversely. In this way, a plywood-like tissue is formed that is reminiscent of isopedine. In a plywood-like tissue, the intrinsic bone fibres of the same layer are parallel to each other, but they differ in their orientation from the fibres of the adjacent layers (e.g. Francillon-Vieillot *et al.* 1990). Under polarized light, those layers in which the fibres are cut approximately longitudinally brighten up and obliterate homogeneously, whereas the layers with fibres aligned perpendicular to the plane of section remain dark and exhibit a very fine bright meshwork that delineates the single fibres. These transversely cut fibres are also clearly visible under non-polarized light as globular structures with the scattered, star-shaped bone cell lacunae in between (Fig. 6D). Some of the fibres possess organic, dark infillings. In their externalmost part, the sculptural saddles appear diffuse dark under polarized light. This is probably caused by Sharpey's fibres and the varying orientation of the intrinsic fibre bundles as described above. More interiorly in the saddles, an irregular stratification of layers with intrinsic fibres orientated parallel and perpendicular to the plane of section is present. The external portion of the cortex is well vascularized mostly by simple primary canals that may anastomose, but also primary and isolated secondary osteons are present. However, the externalmost part of the cortex is avascular. Also the cores of the sculptural saddles are well vascularized by partially anastomosing simple canals and primary osteons. More interiorly in the cortex, the number and size of secondary osteons increase. Some of these possess wide Haversian canals. Zones and annuli cannot be determined in the cortex. Bundles of Sharpey's fibres are conspicuous and fan-shaped in the sculptural saddles, but are absent in the valleys. Compared to *Platyhystrix* (see below), the bundles are thicker and much more densely arranged.

Towards the interior, the secondary osteons increase in number and size, and numerous erosion cavities without a lining of secondary lamellar bone are present. The erosive spaces get abruptly larger more interiorly and attain a rather rounded-square appearance, so that the interior portion of the osteoderm consists of gracile trabeculae that delimit extensive vascular spaces. The trabeculae are composed of parallel-fibred bone in their cores and are lined by secondary lamellar bone. The bone cell lacunae of the trabeculae are long-oval and may exhibit short canaliculi.

Platyhystrix rugosus. This dissorophid is famous for its spectacular 'sail' on top of the neural spines. Each enlarged

neural spine is fused laterally and dorsally to a steep, roof-shaped osteoderm that exceeds the height of the neural spine itself. The external surface of the osteoderms is sculptured with sporadic, mainly dorsoventrally directed ridges that may bifurcate. Tubercles are present in line on the ridges, or are isolated and scattered on the bone surface. In *Platyhystrix*, the osteoderms are basically roof-shaped as in *Aspidosaurus*; however, they have an extremely tall median crest that continues ventrally in a small lateral projection on either lateral side, a short distance dorsal to the level of the zygapophyses (Fig. 1J). For the production of thin sections, the crest was cut horizontally in its dorsal part, i.e. above the neural spine proper.

Histology. The bone histology corresponds basically to that of *Aspidosaurus* with a thin cortex and a trabecular core (Figs 2F and 6E), but the plywood structure in the cortex is developed more regularly.

The external portion of the cortex consists of different, thin layers of parallel fibred bone that constitute a plywood-like structure (Fig. 6F, G). In the region of the rather smooth external surface between the sculptural saddles, the number of successive layers is reduced to three or four, and they appear less well ordered (i.e. the layers may fray out at their boundaries). Towards the flanks of the sculptural saddles, the number of layers increases and their boundaries are well defined. This structure is also present in the bases of the saddles. In its interiormost part, the cortex is rich in secondary osteons that are aligned approximately in a single row in the parts between the sculptural saddles. The scuptural saddles themselves consist to a large degree of coarse parallel-fibred bone whose fibre bundles vary in their dimensions and directions. As in *Aspidosaurus*, the bone matrix of the sculptural saddles is often diffuse in their dorsalmost portion under polarized light. Except for the interiormost portion that contains numerous secondary osteons, the external layer is poorly vascularized. Only sporadic primary vascular canals and scattered primary osteons are present. Loosely arranged, fan-shaped bundles of Sharpey's fibres are visible in the sculptural saddles. Some of the fibres extend interiorly to the layer of secondary osteons. Sharpey's fibres are thinner and very rare in the regions between the sculptural saddles. The bone cell lacunae are spindular in the layers of the plywood structure and exhibit long, branching canaliculi.

In some parts, the cortex exhibits diffuse zones and annuli as in lamellar-zonal bone. At least three annuli are visible and follow the sculpture of the external surface. The middle region is developed as in *Aspidosaurus*.

Cacops aspidephorus. In *Cacops*, the outer morphology of the osteoderms are basically similar to those of *Aspidosaurus*. The roof that is formed by the osteoderm, however, is more flattened, and the dermal sculpture is less pronounced. For histological investigation, the lateral halves of the osteoderm were sectioned in the sagittal plane. Unfortunately, the bone was heavily altered by recrystallization, so nothing can be said about the bone tissue itself, the intrinsic and extrinsic fibres and the vascularization of the compact bone. However, the slides allow the investigation of the osteoderm's microstructure. As in *Platyhystrix* and *Aspidosaurus*, the osteoderms of *Cacops* consist of a thin, compact cortex that encloses a trabecular core with thin trabeculae (Fig. 6H).

Discussion

Differences in osteoderm microstructure and functional considerations

All osteoderms investigated in this study possess basically a microstructure that can be designated as a diploë, i.e. a cancellous or trabecular region is framed externally and internally by a compact cortex of bone, and are therefore similar to the structure of the dermal skull bones in temnospondyls (Bystrow 1935, 1947; Scheyer 2007; personal observations). An exception are the osteoderms of *Plagiosuchus*, that show no clear diploë structure and have a rather compact middle region, that is nevertheless better vascularized than the external and internal regions.

The investigated osteoderms show striking differences in their compactness. The osteoderms of the outgroup, the chroniosuchian *Bystrowiella*, possesses moderately thin compact external and internal cortices, and the large middle region is fine to coarse cancellous. In contrast, *Peltobatrachus* has an extensive external compact cortex that is thicker than the coarse cancellous middle region plus the internal cortex. A similar structure is visible in *Gerrothorax*, in which the thickness of the external and internal cortices is much larger than that of the middle, coarse cancellous to trabecular region. The most compact bone structure is shown by *Plagiosuchus*. In contrast, the osteoderms of the investigated dissorophids *Aspidosaurus*, *Platyhystrix* and *Cacops* are very lightly built with extensive vascular spaces, gracile trabeculae and thin cortices. At least in *Aspidosaurus* and *Platyhystrix*, the cortex is composed of a plywood-like tissue reminiscent of isopedine. This osteoderm structure provides maximum stability and minimum bone mass, and is consistent with the interpretation that the osteoderms of dissorophids served to strengthen the vertebral column during terrestrial locomotion (Dilkes and Brown 2007).

In contrast, the much more massive osteoderms that covered the whole body of *Gerrothorax* and the back of *Plagiosuchus* might be interpreted as serving for reduction of buoyancy and stabilization of the trunk in these aquatic animals. Especially *Gerrothorax* can be regarded as a bottom-dwelling, lurking predator (DeFauw 1989; Schoch and Wild 1999; Hellrung 2003) that shows pachyostosis of the ribs (Castanet *et al.* 2003). Furthermore, in the osteoderms of *Gerrothorax*, the extensive armour probably constituted a calcium reservoir, as indicated by the cyclical resorption events preserved in the external cortex. Similar structures

have been observed in the scales of semionotid fish (Meunier and Gayet 1992) and can be interpreted as a physiological response to periodic changes in salinity of the aquatic environment. Sedimentological studies of the German Lettenkeuper indicate that *Gerrothorax* lived in a large, brackish influenced delta (Schoch and Wild 1999; Hellrung 2003). When the degree of salinity decreased or the animal encountered freshwater, it may have undergone physiological stress, and calcium might have been remobilized from the osteoderms. These periodic changes in salinity might be explained in two ways: either *Gerrothorax* migrated periodically from brackish to freshwater, e.g. for spawning; or *Gerrothorax* remained rather territorial and the salinity changed periodically by input of freshwater from the hinterland, e.g. during the rainy season. We regard the second explanation as the more probable because with its flattened, broad body, the short limbs and short tail, *Gerrothorax* was probably rather inactive and not capable of covering large distances.

In *Peltobatrachus*, whose postcranial morphology suggests a primarily terrestrial mode of life (Panchen 1959), the osteoderms are similarly massive as in *Gerrothorax* and probably served mainly for protection, because they cover the complete dorsal trunk and the anterior part of the tail. Although the osteoderms of *Bystrowiella* are not trabecular and not as lightly built as those of dissorophids, their cortices are rather thin, and the fine to coarse cancellous middle region is quite large and consequently less massive than in plagiosaurids and *Peltobatrachus*. Chroniosuchians were semi-terrestrial animals (Laurin *et al.* 2004), probably feeding in water but capable of land excursions, and the elaborate mechanism of articulation between the osteoderms (Novikov *et al.* 2000; Witzmann *et al.* 2008) may have stabilized the vertebral column.

Dermal sculpture and Sharpey's fibres

The external surface of the osteoderms of *Bystrowiella* is sculptured by a reticular pattern of rounded quadrangular pits, enclosed by ridges (Witzmann *et al.* 2008). In *Aspidosaurus*, the sculpture consists of conspicuous ridges, tubercles and pits, whereas this pattern is attenuated in *Platyhystrix*. A pustular sculpture is present in *Gerrothorax* and *Peltobatrachus*. Thin sections show that the dermal sculpture did not develop by local resorption as suggested for crocodile dermal bones (Buffrénil 1982; but see Vickaryous and Hall 2008), but rather by preferential growth of bone in tubercles and ridges. Growth marks follow clearly the pattern of sculptural saddles and valleys.

Numerous fan-shaped, mineralized Sharpey's fibres are visible in the saddles, whereas they are mostly less abundant or absent in the valleys. The Sharpey's fibres represent extraneous, pre-existing fibres of the dermis that became progressively incorporated in bone during the centrifugal growth of the external cortex. Similar to Sharpey's fibres in mammals (Boyde 1972; Mowbray 2005) and the anchoring fibres in the scales of certain teleosts (Sire 1985, 1986), the pre-existing, strong bundles of Sharpey's fibres in the dermis of basal tetrapods might have induced the preferential growth of bone on the external surface, resulting in the dermal sculpture of tubercles and ridges that became more and more pronounced during ontogeny. The well-mineralized fibres suggest a tight anchorage of the dermis to the external bone surface, especially to the ridges and tubercles. Interestingly, a very similar pattern is visible in the shells of many turtles, in which dense connective tissue is tightly anchored to the sculptural projections of the dermal bones via Sharpey's fibres (e.g. Scheyer and Anquetin 2008). In the scales of many teleosts (Sire 1985, 1986) and osteoderms of lizards (Zylberberg and Castanet 1985; Levrat-Calviac and Zylberberg 1986), anchoring fibres extend uninterrupted from the ossified tissue into the dermis and continue until the basement membrane of the epidermal–dermal boundary. Dense Sharpey's fibres that cross approximately perpendicularly the external cortex of osteoderms and interweave with the collagen fibres of the overlying dermis were also described by Hill (2006) in fossil and extant xenarthran mammals. It can be assumed that the Sharpey's fibres in osteoderms of temnospondyls and *Bystrowiella* likewise extended beyond the bone surface and were interwoven with the fibres of the dermis (and possibly extended until to the epidermal–dermal boundary).

The strong bundles of long Sharpey's fibres in the internal cortex of *Gerrothorax* probably connected the osteoderms to the underlying tendons and muscles of the trunk. In the section of a fairly complete osteoderm, it is visible that the Sharpey's fibres converge towards the centre of the osteoderm, similar to the course of the fibres in phytosaur osteoderms (Scheyer and Sander 2004). Also Hill (2006) reported anchoring Sharpey's fibres in the internal cortex of xenarthrans. A corresponding attachment of the osteoderms to the trunk is visible in *Peltobatrachus*. Similarly strong, anchoring fibres are not present in the internal cortex of *Bystrowiella* and in dissorophids because these osteoderms are tightly attached to the neural spines by co-ossification.

Plagiosuchus bears no dermal sculpture comparable to dermal bones of other basal tetrapods but rather a roughened external surface. The Sharpey's fibres are extensively developed and equally distributed in the external region and directed to the proximal portion of the osteoderm. In the ventral (internal) side of the osteoderm, the Sharpey's fibres are likewise numerous and dense. The extensively developed Sharpey's fibres in *Plagiosuchus* suggest a tight anchorage of the osteoderm within the dermis. The strong fibre bundles in the keel probably connected the osteoderm with the groove in the neural spine.

The mineralized nodules in the dermis of Plagiosuchus

In *Plagiosuchus*, mineralized nodules of irregular outline are preserved on the external surface of the osteoderms and

external to the ventral gastral scales, as well as in all other parts of the trunk, the limbs and the anterior tail. This suggests that the osteoderms (and the gastral scales) in *Plagiosuchus* were located deep within the dermis (probably the stratum compactum), whereas the mineralized nodules were situated in the external part of the dermis (probably the stratum spongiosum). This interpretation might be supported by the absence of the 'typical' dermal sculpture on the external surface of the *Plagiosuchus* osteoderms. For example, only those parts of the osteoderms of the squamate *Anguis fragilis* that are closely located beneath the epidermis bear an external sculpture, whereas those parts that are embedded deeply within the dermis, are rather smooth (Zylberberg and Castanet 1985). Witzmann (2007) suspected that the mineralized nodules might represent vestiges of an extensive armour of osteoderms in *Plagiosuchus*. Alternatively, the nodules might represent an independently evolved structure, in some respects similar to the Eberth–Kastschenko Layer of extant amphibians, but much larger in their dimensions. In any case, the presence of mineralized nodules external to gastral scales and osteoderms in *Plagiosuchus* indicates the presence of a rather thick integument in this temnospondyl.

Interwoven structural fibres and the question of metaplastic tissue

Primary fibrous bone tissue in which the collagenous fibres are aligned obliquely to the bone surface (three-dimensionally interwoven structural fibres, ISF *sensu* Scheyer and Sander 2004; Scheyer 2007; Scheyer and Sánchez-Villagra 2007; Scheyer and Anquetin 2008) is identified in *Bystrowiella* and *Plagiosuchus*. The ISF can be present in the cortices as well as in the middle region, and co-occur with parallel-fibred bone that is mostly coarse and little ordered.

Scheyer and Sander (2004) and Scheyer and Sánchez-Villagra (2007) interpreted ISF in the turtle shell and in dinosaur osteoderms as metaplastic in origin, *sensu* Haines and Mohuiddin (1968). Metaplastic bone develops via direct transformation of pre-existing, dense connective tissue, in the absence of a periost, osteoblasts and osteoid (Vickaryous and Hall 2008). Instead, fibroblasts take over the role of osteoblastic cells, but Scheyer *et al.* (2008) reported the involvement of 'normal' osteoblasts in metaplastic development of the turtle shell. Haines and Mohuiddin (1968) described metaplastic bone as a dense fibrous tissue whose coarse fibres are interwoven and the bone cells arranged irregularly. The bone cell lacunae have mostly short or no canaliculi. Accordingly, the ISF found in the osteoderms of the basal tetrapods investigated here can be interpreted as metaplastic tissue. However, none of the osteoderms (with the exception of *Gerrothorax* and *Peltobatrachus* whose primary bone tissue is solely composed of parallel-fibred bone) are composed of a uniform bone tissue with a consistent histology. As Main *et al.* (2005) emphasized, many intermediate states exist between the two extremes, the periosteal bone of 'normal intramembranous bone' and the metaplastic bone, and transitions from metaplastic to periosteal can be observed in the same section (e.g. ISF to parallel-fibred bone; see also Scheyer and Sánchez-Villagra 2007). Also Goodwin and Horner (2004) found islets of metaplastic tissue within the periosteal bone in the skull of pachycephalosaur dinosaurs. Whereas woven or fibrous bone, which shows general isotropy in polarized light, is associated with a fast deposition of bone (e.g. Francillon-Vieillot *et al.* 1990; Ricqlès *et al.* 1991), no data are available concerning the growth rate of ISF (Scheyer and Sánchez-Villagra 2007). However, the often rounded shape of the bone cell lacunae and their unordered arrangement in ISF of the osteoderms investigated here could suggest a rather rapid growth rate.

Development of bone via metaplasia requires a dense tissue such as articulation facets, attachment sites of tendons and ligaments, or a dense dermis (Haines and Mohuiddin 1968). The occurrence of metaplastic tissue in the osteoderms of basal tetrapods investigated here might indicate that the dermis was rather dense and composed of an interwoven network of strong collagenous fibre bundles. This interpretation of a dense integument is further supported by the mostly closely packed, thick bundles of Sharpey's fibres that extended from the bone surface into the dermis and certainly led to a strengthening and tight attachment of the dermis to the outer bone surface (see above).

Metaplastic development has been proposed for the osteoderms of several tetrapods such as extant squamates (Zylberberg and Castanet 1985; Levrat-Calviac and Zylberberg 1986), fossil and extant archosaurs (e.g. Ricqlès *et al.* 2001; Scheyer and Sander 2004; Main *et al.* 2005; Vickaryous and Hall 2008), in dermal bones of the turtle shell (Scheyer and Sánchez-Villagra 2007), as well as in extant anurans (Ruibal and Shoemaker 1984). Whereas Vickaryous and Hall (2006) found no evidence of metaplasia in osteoderms of the extant armadillo *Dasypus*, Hill (2006) demonstrated characteristics of metaplastic tissue in fossil and extant xenarthran osteoderms. In contrast to the tetrapod groups listed above, the postcranial armour plates of fishes (Sire and Huysseune 2003) show a 'normal' periosteal development without evidence of metaplasia.

Phylogenetic considerations

Recent phylogenetic analyses of basal tetrapods suggest that the osteoderms in dissorophids, plagiosaurids, and chroniosuchians evolved independently (Yates and Warren 2000; Ruta *et al.* 2003; Anderson *et al.* 2008). This is also indicated by the unique structure of the osteoderms in *Aspidosaurus*, *Platyhystrix* and probably *Cacops*, that might be a synapomorphy of dissorophids. In *Gerrothorax*, the structure of the osteoderms corresponds largely to those of the dermal skull roof (personal observations) and consists mainly of periosteal parallel-fibred bone. Most similar to this structure is the osteoderm histology of *Peltobatrachus*, with an extensively thick external cortex and strong Sharpey's fibre bundles

penetrating the thinner internal cortex. Furthermore, both taxa have a tubular dermal sculpture that is, nevertheless, columnar in *Peltobatrachus*. These features might support the proposed close relationship of *Peltobatrachus* and plagiosaurids (Panchen 1959; Milner 1990); however, pustular sculpture on osteoderms occurs also in several chroniosuchians (Novikov *et al.* 2000), and some of the common features of *Gerrothorax* and *Peltobatrachus* might have functional explanations: the thick cortex might have served for protection, and the large bundles of Sharpey's fibres in the internal cortex anchored the osteoderms to the subdermal connective tissue, because no co-ossification with endoskeletal elements is present. Within plagiosaurids, however, the described differences in histological structure and morphogenesis of the osteoderms in *Gerrothorax* and *Plagiosuchus* suggest an iterative evolution of osteoderms. Whereas in *Gerrothorax* the osteoderms show a 'regular' diploë structure, this is absent in *Plagiosuchus*. Furthermore, the osteoderms of *Gerrothorax* are composed of periosteal parallel-fibred bone. In contrast, the osteoderms of *Plagiosuchus* comprise large parts of interwoven structural fibres.

In summary, the histology of the investigated osteoderms suggests an independent development of the osteoderms in chroniosuchians (*Bystroviella*), among the plagiosaurids *Gerrothorax* and *Plagiosuchus*, and in dissorophids. It cannot be ruled out that the osteoderms of *Gerrothorax* and *Peltobatrachus* are inherited from a common ancestor. The independent acquisition of osteoderms in different lineages of basal tetrapods reflects the potential of the dermis in tetrapods to develop skeletal structures. Additional to the dermal scales in basal tetrapods that probably represent a heritage from non-tetrapod ancestors (Witzmann 2007) and the large plate-like osteoderms of armoured temnospondyls and chroniosuchians described in this study, small, irregular osteoderms have been reported among temnospondyls locally in the trunk or gular region of dvinosaurians (*Trimerorhachis*: R. R. Schoch, personal communication; *Isodectes*: AMNH 11037; *Acroplous*: Englehorn *et al.* 2008; *Thabanchaia*: Warren 1999), zatracheids (Langston 1953; Schoch 1997), *Platyrhinops* (Carroll 1964), probably *Edops* (Romer and Witter 1942), and certain stereospondyls (*Laidleria*: Kitching 1957; *Sclerothorax*: von Huene 1932), as well as in some microsaurs (Carroll and Gaskill 1978). The skeletogenic potential of the tetrapod dermis is also shown by extant anurans in which osteoderms evolved independently within different lineages (Ruibal and Shoemaker 1984), as well as in several groups of amniotes (e.g. Scheyer and Sander 2004; Hill 2005, 2006; Vickaryous and Hall 2006, 2008). According to Main *et al.* (2005) and Vickaryous and Hall (2008), a deep homology exists between osteoderms in the different tetrapod lineages because they have a common origin in the skeletogenic potential of the dermis. The advantages of osteoderms are manifold (like support of the vertebral column, the reduction of buoyancy, physiological calcium reservoir, and simply protection against predators). The data derived from the quite distantly related chroniosuchian *Bystroviella* and the temnospondyl *Plagiosuchus* suggest that the potential for metaplastic ossification in the dermis was already present in several lineages of early tetrapods, a feature that has so far not been detected in fish (Sire and Huysseune 2003).

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References

Anderson, J. S., Reisz, R. R., Scott, D., Fröbisch, N. B. and Sumida, S. S. 2008. A stem batrachian from the Early Permian of Texas and the origin of frogs and salamanders. – *Nature* **453**: 515–518.

Berman, D. S. and Lucas, S. G. 2003. *Aspidosaurus binasser* (Amphibia, Temnospondyli), a new species of Dissorophidae from the Lower Permian of Texas. – *Annals of the Carnegie Museum* **72**: 241–262.

Bolt, J. 1974. Armor of dissorophids (Amphibia: Labyrinthodontia): an examination of its taxonomic use and report of a new occurrence. – *Journal of Paleontology* **48**: 135–142.

Boyde, A. 1972. Scanning electron microscopic studies of bone. In Bourne, G. (Ed.): *The Biochemistry and Physiology of Bone*, Vol. 1, pp. 259–309. Academic Press, New York.

Broili, F. 1904. Permische Stegocephalen und Reptilien aus Texas. – *Palaeontographica* **51**: 1–16.

Buffrénil, V. de 1982. Morphogenesis of bone ornamentation in extant and extinct crocodilians. – *Zoomorphologie* **99**: 155–166.

Buffrénil, V. de, Farlow, J. O. and Ricqlès, A. de 1986. Growth and function of *Stegosaurus* plates: evidence from bone histology. – *Paleobiology* **12**: 459–473.

Bystrow, A. P. 1935. Morphologische Untersuchungen der Deckknochen des Schädels der Stegocephalen. 1. Mitteilung. Schädel der Stegocephalen. – *Acta Zoologica (Stockholm)* **16**: 65–141.

Bystrow, A. P. 1944. *Kotlassia prima* Amalitzky. – *Bulletin of the Geological Society of America* **1944**: 379–416.

Bystrow, A. P. 1947. Hydrophilous and xerophilous labyrinthodonts. – *Acta Zoologica (Stockholm)* **28**: 137–164.

Carroll, R. L. 1964. Early evolution of the dissorophid amphibians. – *Bulletin of the Museum of Comparative Zoology, Harvard University* **131**: 161–250.

Carroll, R. L. and Gaskill, P. 1978. *The Order Microsauria*. The American Philosophical Society, Philadelphia.

Castanet, J., Francillon-Vieillot, H., Ricqlès, A. de and Zylberberg, L. 2003. The skeletal histology of the Amphibia. In Heatwole, H. and Davies, M. (Eds): *Amphibian Biology*, volume 5: *Osteology*, pp. 1598–1683. Surrey Beatty, Chipping Norton.

Chinsamy, A. and Raath, M. A. 1992. Preparation of bone for histological study. – *Palaeontologia Africana* **29**: 39–44.

DeFauw, S. L. 1989. Temnospondyl amphibians: a new perspective on the last phases in the evolution of the Labyrinthodontia. – *Michigan Academician* **21**: 7–32.

DeMar, R. 1966. The phylogenetic and functional implications of the armor of the Dissorophidae. – *Fieldiana: Geology* **16**: 55–88.

DeMar, R. 1968. The Permian labyrinthodont amphibian *Dissorophus multicinctus*, and adaptations and phylogeny of the family Dissorophidae. – *Journal of Paleontology* **42**: 1210–1242.

Dilkes, D. and Brown, L. E. 2007. Biomechanics of the vertebrae and associated osteoderms of the Early Permian amphibian *Cacops aspidephorus*. – *Journal of Zoology* **271**: 396–407.

Englehorn, J., Small, B. J. and Huttenlocker, A. 2008. A redescription of *Acroplous vorax* (Temnospondyli: Dvinosauria) based on new specimens from the Early Permian of Nebraska and Kansas, USA. – *Journal of Vertebrate Paleontology* **28**: 291–305.

Francillon-Vieillot, H., de Buffrénil, V., Castanet, J., Geraudie, J., Meunier, F. J., Sire, J.-Y., Zylberberg, L. and de Ricqlès, A. 1990. Microstructure and mineralization of vertebrate skeletal tissues. In Carter, J. G. (Ed.): *Biomineralization: Patterns and Evolutionary Trends*, pp. 471–530. – Van Nostrand Reinhold, New York.

Golubev, V. K. 1998. Narrow-armored chroniosuchians (Amphibia, Anthracosauromorpha) from the Late Permian of Eastern Europe. – *Paleontological Journal* **32**: 278–287.

Golubev, V. K. 2000. Permian and Triassic chroniosuchians and biostratigraphy of Upper Tatarian beds of European Russia based on tetrapods. – *Trudy Paleontologicheskoso Instituta Rossijskaja Akademyia Nauk* **276**: 1–174.

Goodwin, M. B. and Horner, J. R. 2004. Cranial histology of pachycephalosaurs (Ornithischia: Marginocephalia) reveals transitory structures inconsistent with head-butting behavior. – *Paleobiology* **30**: 252–267.

Gubin, Y. 1980. New Permian dissorophids of the Ural forelands. – *Paleontological Journal* **1980**: 88–96.

Haines, R. W. and Mohuiddin, A. 1968. Metaplastic bone. – *Journal of Anatomy* **103**: 527–538.

Hellrung, H. 2003. *Gerrothorax pustuloglomeratus*, ein Temnospondyle (Amphibia) mit knöchernen Branchialkammer aus dem Unteren Keuper von Kupferzell (Süddeutschland). – *Stuttgarter Beiträge zur Naturkunde, Serie B* **330**: 1–130.

Hill, R. V. 2005. Integration of morphological data sets for phylogenetic analysis of Amniota: the importance of integumentary characters and increased taxonomic sampling. – *Systematic Biology* **54**: 1–18.

Hill, R. V. 2006. Comparative anatomy and histology of xenarthran osteoderms. – *Journal of Morphology* **267**: 1441–1460.

Huene, F. von 1932. Ein neuartiger Stegocephalen-Fund aus dem oberhessischen Buntsandstein. – *Paläontologische Zeitschrift* **14**: 200–229.

Jones, S. J. and Boyde, A. 1974. The organization and gross mineralization patterns of the collagen fibres in Sharpey fibre bone. – *Cell Tissue Research* **148**: 83–96.

Kitching, J. W. 1957. A small stereospondylous labyrinthodont from the Triassic beds of South Africa. – *Palaeontologia Africana* **5**: 67–82.

Langston, W. 1953. Permian amphibians from New Mexico. – *University of California Publications in Geological Sciences* **29**: 349–416.

Laurin, M. 2000. Seymouriamorphs. In Heatwole, H. and Carroll, R. L. (Eds): *Amphibian Biology*, volume 4: *Paleontology*, pp. 1064–1080. Surrey Beatty, Chipping Norton.

Laurin, M., Girondot, M. and Loth, M.-M. 2004. The evolution of long bone microstructure and lifestyle in lissamphibians. – *Paleobiology* **30**: 589–613.

Levrat-Calviac, V. and Zylberberg, L. 1986. The structure of the osteoderms in the gekko: *Tarentola mauritanica*. – *American Journal of Anatomy* **176**: 437–446.

Lewis, G. E. and Vaughn, P. P. 1965. Early Permian vertebrates from the Cutler Formation of the Placerville Area Colorado. – *United States Geological Survey Professional Paper* **503**: 1–46.

Li, J.-L. and Cheng, Z.-W. 1999. New anthracosaur and temnospondyl amphibians from Gansu, China – the fifth report on Late Permian Dashankou lower tetrapod fauna. – *Vertebrata Palasiatica* **37**: 242–247.

Main, R. P., Ricqlès, A. de, Horner, J. R. and Padian, K. 2005. The evolution and function of thyreophoran dinosaur scutes: implications for plate function in stegosaurs. – *Paleobiology* **31**: 291–314.

Meunier, F. J. and Gayet, M. 1992. Nouveau remaniement de la ganoine chez un Semionodontidae du Crétacé supérieur de Bolivie: intérprêtations paléobiologiques. – *Geobios* **25**: 767–774.

Milner, A. R. 1990. The radiations of temnospondyl amphibians. In Taylor, P. D. and Larwood, G. P. (Eds): *Major Evolutionary Radiations. Systematics Association Special*, Vol. 42, pp. 321–349. – Clarendon Press, Oxford.

Mowbray, K. 2005. Surface bone histology of the occipital bone in humans and chimpanzees. – *Anatomical Record B* **283**: 14–22.

Nilsson, T. 1946. A new find of *Gerrothorax rhaeticus* Nilsson, a plagiosaurid from the Rhaetic of Scania. – *Lunds Universitets Årsskrift, Ny Följd* **42**: 1–43.

Novikov, I. V., Shishkin, M. A. and Golubev, V. K. 2000. Permian and Triassic anthracosaurs from Eastern Europe. In Benton, M., Shishkin, M. A., Unwin, D. and Kurochkin, E. (Eds): *The Age of Dinosaurs in Russia and Mongolia*, pp. 60–70. Cambridge University Press, Cambridge.

Panchen, A. 1959. A new armoured amphibian from the Upper Permian of East Africa. – *Philosophical Transactions of the Royal Society of London, Series B* **242**: 207–281.

Ricqlès, A. de, Meunier, F. J., Castanet, J. and Francillon-Vieillot, H. 1991. Comparative microstructure of bone. In Hall, B. K. (Ed.): *Bone*, volume 3: *Bone Matrix and Bone Specific Products*, pp. 1–78. CRC Press, Boca Raton.

Ricqlès, A. de, Pereda Superbiola, X., Gasparini, Z. and Olivero, E. 2001. Histology of dermal ossifications in an ankylosaurian dinosaur from the Late Cretaceous of Antarctica. – *Asociación Paleontológica Argentina, Publicación Especial* **7**: 171–174.

Romer, A. S. and Witter, V. 1942. *Edops*, a primitive rhachitomous amphibian from the Texas Red Beds. – *Journal of Geology* **50**: 925–960.

Ruibal, R. and Shoemaker, V. 1984. Osteoderms in anurans. – *Journal of Herpetology* **18**: 313–328.

Ruta, M. and Coates, M. I. 2007. Dates, nodes and character conflict: addressing the lissamphibian origin problem. – *Journal of Systematic Paleontology* **5**: 69–122.

Ruta, M., Coates, M. I. and Quicke, D. L. J. 2003. Early tetrapod relationships revisited. – *Biological Reviews of the Cambridge Philosophical Society* **78**: 251–345.

Scheyer, T. M. 2007. Skeletal histology of the armor of the Placodontia: the occurrence of 'postcranial fibro-cartilaginous bone' and its developmental implications. – *Journal of Anatomy* **211**: 737–753.

Scheyer, T. M. and Anquetin, J. 2008. Bone histology of the Middle Jurassic turtle shell remains from Kirtlington, Oxfordshire, England. – *Lethaia* **41**: 85–96.

Scheyer, T. M. and Sander, P. M. 2004. Histology of ankylosaur osteoderms: implications for systematics and function. – *Journal of Vertebrate Paleontology* **24**: 874–893.

Scheyer, T. M. and Sánchez-Villagra, M. R. 2007. Carapace bone histology in the giant pleurodiran turtle *Stupendemys geographicus*: phylogeny and function. – *Acta Palaeontologica Polonica* **52**: 137–154.

Scheyer, T. M., Brüllmann, B. and Sánchez-Villagra, M. R. 2008. The ontogeny of the shell in side-necked turtles, with emphasis on the homologies of costal and neural bones. – *Journal of Morphology* **269**: 1008–1021.

Schoch, R. R. 1997. Cranial anatomy of the Permian temnospondyl amphibian *Zatrachys serratus* Cope 1878, and the phylogenetic position of the Zatrachydidae. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **206**: 223–248.

Schoch, R. R. and Milner, A. R. 2004. Structure and implications of theories on the origin of lissamphibians. In Arratia, G., Wilson, M. V. H. and Cloutier, R. (Eds): *Recent Advances in the Origin and Early Radiation of Vertebrates.*, pp. 345–377. Dr. Friedrich Pfeil, München.

Schoch, R. R. and Wild, R. 1999. Die Wirbeltier-Fauna im Keuper von Süddeutschland. In Hauschke, N. and Wilde, V. (Eds): *Die Trias – Eine Ganz Andere Welt*, pp. 395–408. Dr. Friedrich Pfeil, München.

Sire, J.-Y. 1985. Fibres d'ancrage et couche limitante externe à la surface des écailles du Cichlidae *Hemichromis bimaculatus* (Téléostéen, Perciforme): données ultrastructurales. – *Annales des Sciences Naturelles, Zoologie*, **13e Série** 7: 163–180.

Sire, J.-Y. 1986. Ontogenic development of surface ornamentation in the scales of *Hemichromis bimaculatus* (Cichlidae). – *Journal of Fish Biology* **28**: 713–724.

Sire, J.-Y. and Huysseune, A. 2003. Formation of dermal skeletal and dental tissues in fish: a comparative and evolutionary approach. – *Biological Reviews of the Cambridge Philosophical Society* **78**: 219–249.

Toledo, R. C. and Jared, C. 1993. Cutaneous adaptations to water balance in amphibians. – *Comparative Biochemistry and Physiology* **105A**: 593–608.

Vallin, G. and Laurin, M. 2004. Cranial morphology and affinities of *Microbrachis*, and a reappraisal of the phylogeny and lifestyle of the first amphibians. – *Journal of Vertebrate Paleontology* **24**: 56–72.

Vickaryous, M. K. and Hall, B. K. 2006. Osteoderm morphology and development in the Nine-Banded Armadillo, *Dasypeps novemcinctus* (Mammalia, Xenarthra, Cingulata). – *Journal of Morphology* **267**: 1273–1283.

Vickaryous, M. K. and Hall, B. K. 2008. Development of the dermal skeleton in *Alligator mississippiensis* (Archosauria, Crocodylia) with comments on the homology of osteoderms. – *Journal of Morphology* **269**: 398–422.

Wake, M. H. and Nygren, K. M. 1987. Variation in scales in *Dermophis mexicanus* (Amphibia: Gymnophiona): are scales of systematic utility? *Fieldiana* **1378**: 1–8.

Warren, A. A. 1999. Karroo tupilakosaurid: a relict from Gondwana. – *Transactions of the Royal Society of Edinburgh, Earth Sciences* **89**: 145–160.

Warren, A. A. 2000. Secondarily aquatic temnospondyls of the Upper Permian and Mesozoic. In Heatwole, H. and Carroll, R. L. (Eds): *Amphibian Biology*, volume 4: *Palaeontology*, pp. 1121–1149. Surrey Beatty, Chipping Norton.

Williston, S. W. 1910. *Cacops*, *Dasmospondylus*: new genera of Permian verebrates. – *Bulletin of the Geological Society of America* **21**: 249–284.

Witzmann, F. 2005. A dissorophid temnospondyl in the Upper Permian Kupferschiefer of Germany. – *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 5: 289–300.

Witzmann, F. 2007. The evolution of the scalation pattern in temnospondyl amphibians. – *Zoological Journal of the Linnean Society London* **150**: 815–834.

Witzmann, F., Schoch, R. R. and Maisch, M. 2008. A relict basal tetrapod from Germany: first evidence of a Triassic chroniosuchian outside Russia. – *Naturwissenschaften* **95**: 67–72.

Yates, A. M. and Warren, A. A. 2000. The phylogeny of the 'higher' temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. – *Zoological Journal of the Linnean Society* **128**: 77–121.

Zylberberg, L. and Castanet, J. 1985. New data on the structure and the growth of the osteoderms in the reptile *Anguis fragilis* L. (Anguidae, Squamata). – *Journal of Morphology* **186**: 327–342.

Zylberberg, L., Castanet, J. and Ricqlès, A. de 1980. Structure of the dermal scales in Gymnophiona (Amphibia). – *Journal of Morphology* **165**: 41–54.

Zylberberg, L. and Wake, M. H. 1990. Structure of the scales of *Dermophis* and *Microcaecilia* (Amphibia: Gymnophiona), and a comparison to dermal ossifications of other vertebrates. – *Journal of Morphology* **206**: 25–43.

Histology and external structure of osteoderms in early tetrapods

Appendix 7

Buchwitz, M., **Witzmann, F.**, Voigt, S. & Golubev, V. 2012. Osteoderm microstructure indicates the presence of a crocodylian-like trunk bracing system in a group of armoured basal tetrapods. – Acta Zoologica (Stockholm) 93: 260–280.

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Osteoderm microstructure indicates the presence of a crocodylian-like trunk bracing system in a group of armoured basal tetrapods

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Abstract

Buchwitz, M., Witzmann, F., Voigt, S. and Golubev, V. 2012. Osteoderm microstructure indicates the presence of a crocodylian-like trunk bracing system in a group of armoured basal tetrapods. —*Acta Zoologica* (Stockholm) **93**: 260–280.

The microstructure of dorsal osteoderms referred to the chroniosuchid taxa *Chroniosuchus*, *Chroniosaurus*, *Madygenerpeton* and cf. *Uralerpeton* is compared to existing data on the bystrowianid chroniosuchian *Bystrowiella* and further tetrapods. Chroniosuchid osteoderms are marked by thin internal and relatively thick external cortices that consist of lowly vascularised parallel-fibred bone. They are structured by growth marks and, in case of *Madygenerpeton*, by lines of arrested growth. The cancellous middle region is marked by a high degree of remodelling and a primary bone matrix of parallel-fibred bone that may include domains of interwoven structural fibres. Whereas the convergence of *Bystrowiella* and chroniosuchid osteoderms is not confirmed by our observations, the internal cortex of the latter displays a significant peculiarity: It contains distinct bundles of shallowly dipping Sharpey's fibres with a cranio- or caudoventral orientation. We interpret this feature as indicative for the attachment of epaxial muscles which spanned several vertebral segments between the medioventral surface of the osteoderms and the transversal processes of the thoracic vertebrae. This finding endorses the hypothesis that the chroniosuchid osteoderm series was part of a crocodylian-like trunk bracing system that supported terrestrial locomotion. According to the measured range of osteoderm bone compactness, some chroniosuchian species may have had a more aquatic lifestyle than others.

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Introduction

Chroniosuchians are a group of anamniote tetrapods whose fossils have been discovered within Permian and Triassic continental successions of Europe and Asia. They constituted an abundant faunal element in the tetrapod assemblages of Eastern Europe throughout the Late Permian and survived there up to the Middle Triassic (Sennikov 1996; Golubev 2000; Novikov *et al.* 2000). Isolated occurrences from the Middle and the Late Permian of China (Young 1979; Li and Cheng 1999), from the Middle Triassic of south-west Germany (Witzmann *et al.* 2008), and from the Middle to early Late Triassic of Kyrgyzstan, Middle Asia (Schoch *et al.* 2010), indicate a wider geographical distribution despite the limited variety of the group (12 valid Russian species, see Novikov *et al.* 2000; four more non-Russian species).

On the basis of their vertebral structure and skull morphology, chroniosuchians have been classified either as seymouriamorphs (Tatarinov 1972) or as embolomere relatives (Ivakhnenko and Tverdokhlebova 1980; most following works) prior to their consideration in cladistic analyses. Recent cladistic approaches confirmed their belonging to the amniote stem-group (*sensu* Ruta *et al.* 2003), whereas their close relationship with embolomeres or another reptiliomorph group is still under discussion (Clack and Klembara 2009; Klembara *et al.* 2010; Schoch *et al.* 2010; Fig. 1A,B). According to the lepospondyl hypothesis of lissamphibian ancestry, seymouriamorphs, embolomeres and further related

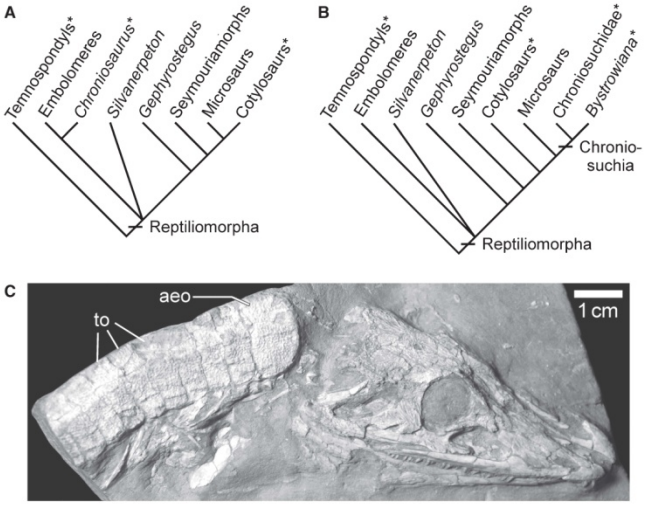

Fig. 1—Relationships and appearance of the Chroniosuchia. —**A, B.** Cladograms for the crown-group Tetrapoda according to recent phylogenetic hypotheses considering chroniosuchians. —**A.** Relationships simplified after the tree of Klembara *et al.* (2010). —**B.** Simplified after Schoch *et al.* (2010). The occurrence of a dorsal osteoderm system in some or all members of a group is denoted with an asterisk. —**C.** Anterior skeleton of the chroniosuchid *Chroniosaurus dongusensis* (specimen PIN 3585/124), displaying the anterior part of the osteoderm shield.

groups–chroniosuchians probably included–would not be part of the amniote stem but lie outside the tetrapod crown-group (Laurin and Reisz 1997; Vallin and Laurin 2004). Two major subtaxa of the Chroniosuchia have been defined, mainly on the basis of their distinct osteoderm morphologies (see Golubev 1998; Novikov and Shishkin 2000): 'Chroniosuchidae' and 'Bystrowianidae' were erected by V'yushkov (1957*a,b)* as two families of batrachosaurs which he did not regard as closely related. Later, Ivakhnenko and Tverdokhlebova (1980) joined the two groups within the Chroniosuchia (=Chroniosuchida, Tatarinov 1972). Including *Bystrowiana permira* (V'yushkov 1957*b*) as the only better known bystrowianid and four chroniosuchid taxa, the analysis of Schoch *et al.* (2010) recovered Chroniosuchia as a monophyletic group comprising *Bystrowiana* and Chroniosuchidae as sister taxa.

This approach is dedicated to a key feature of chroniosuchians – a single dorsal series of highly characteristic osteoderms, beginning with an axially elongated anterior-end osteoderm in contact with the skull, which is followed by numerous shorter osteoderms along the animal's back (Fig. 1C). As in the osteoderm series of the plagiosaurid temnospondyl *Plagiosuchus pustuliferus* (Fraas 1896), the ventral side of each chroniosuchian osteoderm bears a medial keel, the *processus ventralis*, which formed the connection to one corresponding vertebra (as reconstructed by Ivakhnenko and Tverdokhlebova 1980; fig. 12). Unlike the condition in *P. pustuliferus* (see Witzmann and Soler-Gijón 2010), however, the chroniosuchian *processus ventralis* was not accommodated by an incision of the neural arch. Instead, it was either co-ossified with the neural spine via a horizontal suture (in bystrowianids) or forming a deep indentation enclosing the neural spine (in chroniosuchids; Golubev 1998*a*).

A peculiarity of the chroniosuchian osteoderm series with relevance for the functional interpretation of their histological properties is the articulation of each two neighbouring plates. Unlike the very slight overlap of successive dorsal osteoderms in *P. pustuliferus* (Witzmann and Soler-Gijón 2010) and the more considerable overlap in the osteoderm double row of some dissorophid temnospondyls (Dilkes and Brown 2007; Dilkes 2009), the articulation in chroniosuchians is marked by a multifold overlap of complexly interlocking osteoderm processes. In chroniosuchids, it involves the axially elongated ventral process (*processus ventralis*), a pair of anterior wings (*alae anteriores/processus articulares anteriores*) and a corresponding pair of posteroventral wing facets (*facies alares*), a pair of posterior processes (*processus articulares posteriores*) and a corresponding anteroventral depression (*depressio ventralis*) on the central body, and the corresponding posterodorsal and anteroventral facets on the lateral osteoderm wings (*alae scutulumi*) (Golubev 1998; Novikov and Shishkin 2000; overlapping parts are grey-shaded in Fig. 2A). The osteoderm articulation in bystrowianid chroniosuchians is defined by enlarged anterior wings and wing facets, and an often shelf-like posterior articular plate (*lamina articularis*) which is accommodated by an anteroventral depression (*depressio ventralis*), but it lacks the lateral osteoderm wings (*alae scutulumi*).

Apart from the interpretation that the osteoderms supported thermoregulation (Hartmann-Weinberg 1935), the function of the osteoderm system was not explicitly addressed in early approaches on chroniosuchians, but the term 'armour' and the hypothesis that a trilobite-like curling of the animal was possible (Ivakhnenko and Tverdokhlebova 1980, p. 25) imply that the broad osteoderm systems of chroniosuchids were regarded as protection carapaces. Recently, the

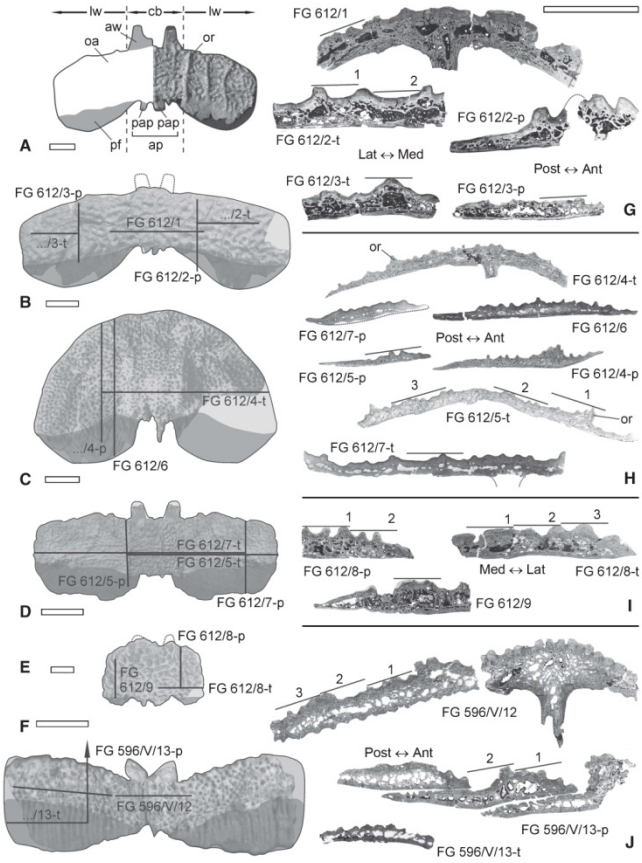

Fig. 2—Chroniosuchian osteoderm morphology, position and overview images for all considered thin sections. —**A.** Terminology of chroniosuchid osteoderm features for the exemplary specimen PIN 523/20 (after Golubev 1998; Novikov and Shishkin 2000). Overlap areas are grey-shaded. —**B**–**F**. Exemplary chroniosuchid osteoderms in dorsal view, belonging to the species *Chroniosuchus paradoxus* (SGU 104B/646, B), *Chroniosaurus dongusensis* (PIN 3713/39 in C; PIN 3585/119 in D), *Uralerpeton tverdochlebovae* (PIN 1100/8, E), and *Madygenerpeton pustulatus* (FG 596/V/5, F). The posterodorsal facets are marked in dark grey. —**G**–**J.** Overview images of osteoderm thin sections marked in B–F, sorted according to taxa. —**G**. *Chroniosuchus licharevi*. —**H**. *Chroniosaurus dongusensis*. —**I**. cf. *Uralerpeton tverdochlebovae*. —**J**. *Madygenerpeton pustulatus*. Suffixes '-p' and '-t' refer to parasagittal and transversal sections, respectively. Thin black bars and numbers 1–3 mark the positions of sections considered for compactness analysis. Dotted lines designate outlines of fragmented osteoderms. All scale bars equal 1 cm.

elaborateness of articulation led to the hypothesis that the osteoderm series functioned as a support device for the axial skeleton and musculature – in agreement with a lifestyle that included some terrestrial locomotion (Clack and Klembara 2009; Buchwitz and Voigt 2010; Witzmann and Soler-Gijón 2010). Whereas the lack of articulated hand and foot skeletons is a hindering factor for the interpretation of chroniosuchian locomotion, lifestyle and the role of their osteoderm systems, another indication was provided by studies on the long bone histology of basal tetrapods which found the bone compactness profile of the chroniosuchian *Chroniosaurus dongusensis* (Tverdokhlebova 1972) to be that of a terrestrial or semi-terrestrial animal (Laurin *et al.* 2004, 2006; Kriloff *et al.* 2008).

Seventy years earlier, Hartmann-Weinberg (1935) published the first histological study on chroniosuchid osteoderms, which were falsely referred to the seymouriamorph *Kotlassia prima* (Amalitzky 1921) by that time. However, as pointed out by Bystrow (1940), she misinterpreted some part of the osteoderm bone as dentine layers similar to those of crossopterygian cosmoid scales, leading her to wrong conclusions regarding lifestyle, palaeoenvironment and homology with skeletal elements of other tetrapods. Only one other study provides further histological data on the osteoderms: Witzmann and Soler-Gijón (2010) include a sample of the bystrowianid *Bystrowiella schumanni* (Witzmann *et al.* 2008). They found that its limited similarity with the osteoderm types of different temnospondyl taxa allows no simple functional or ecological conclusions by analogy.

Given the lack of recent histological data on chroniosuchid osteoderms, this approach focuses on a detailed description of the osteoderm bone tissues occurring in the Chroniosuchidae. We are comparing four chroniosuchid taxa, each on the basis of several osteoderms, to address the following issues: (1)

indications for the homology of chroniosuchid and *Bystrowiella* osteoderms; (2) the mode of skeletogenesis; (3) palaeobiological implications from osteoderm development; (4) the structure of adjacent soft tissues and osteoderm-osteoderm joints and how they might have constrained the mechanics of the osteoderm system; and (5) palaeoecological inference from the analysis of bone compactness.

Institutional abbreviations

FG, Geological Institute of the TU Bergakademie, Freiberg, Germany; MCZ, Museum of Comparative Zoology, Harvard, Cambridge, MA, USA; PIN, Borissyak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; SGU, Saratov State University, Saratov, Russia; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; THU, Teikyo Heisei University, Ichihara City, Chiba Prefecture, Japan.

Anatomical abbreviations

aeo, anterior-end osteoderm; ant, anterior; ap, articular plate; aw, anterior wings; cb, central body; cl, cancellous layer; cpfb, coarse parallel-fibred bone; ec, external cortex; ic, internal cortex; ice, intercentrum; isf, interwoven structural fibres; lat, lateral; lb, lamellar bone; lw, lateral wings; med, medial; na, neural arch; oa, ornamented dorsal area; or, ornamentation ridge; pap, posterior articulation process; pce, pleurocentrum; pf, posterodorsal facet; pfb, (homogenous) parallel-fibred bone; post, posterior; shf, Sharpey's fibres; to, trunk osteoderm; tp, transversal process; vp, ventral process.

Materials

Our histological description involves the following chroniosuchid taxa and specimens (Table 1, Fig. 2B–J; see also list in Golubev 2000, p. 7–8, for the Russian localities):

1 *Chroniosuchus lichareví* (Riabinin and Shishkin 1962): FG 612/1 to 3, three fragments of trunk osteoderms from the Lopingian (Tatarian Series, Upper Vyatkian Substage, *Chroniosuchus paradoxus* Tetrapod Zone) of Gorokhovets, a locality in the Vladimir Region, European part of Russia. These form a part of a larger assemblage of tetrapod remains (Sennikov *et al.* 2003) including cranial and postcranial material of the chroniosuchid *Chroniosuchus lichareví* which has not yet been described in detail.
2 *Chroniosaurus dongusensis*: FG 612/4 to 7, two osteoderms from each of two classical chroniosuchid localities of the Lopingian (Tatarian Series, Upper Severodvinian Substage, *Chroniosaurus dongusensis* Tetrapod Zone): (1) Dongus-6, Orenburg Region, and (2) Poteryakha-2, Vologda Region, both in the European part of Russia. Only for *C. dongusensis*, we obtained samples of the half-moon-shaped anterior-end osteoderms (Fig. 2C), whose ornamentation is similar to that of the trunk osteoderm series.
3 cf. *Uralerpeton tverdochlebovae* (Golubev 1998): FG 612/8 and 9, two osteoderm fragments from the Lopingian strata (Tatarian Series, Upper Vyatkian Substage, *Archosaurus rossicus* Tetrapod Zone) of Vyazniki-1, a locality in the Vladimir Region, European part of Russia. The same locality also yielded material of another chroniosuchian, *Bystrowiana permira*, and we conditionally assign FG 612/8 and FG 612/9 to *Uralerpeton tverdochlebovae* and not to *Bystrowiana permira* because of (1) a diagonal ventral ridge in FG 612/9, which is reminiscent of an osteoderm crest only occurring in chroniosuchids (*crista scutulumi ventralis externa*, see Golubev 1998) and (2) the meddled appearance of the dorsal ornament which is unlike the more regular polygonal pattern in *Bystrowiana* (see Golubev 2000 for examples of both species).
4 *Madygenerpeton pustulatus* (Schoch *et al.* 2010): FG 596/V/12, an isolated fragmentary osteoderm, and FG 596/V/13, a series of three adjacent osteoderms, from the

Table 1 Taxonomic assignment, inventory number, locality, stratigraphy, and relevant morphological data of specimens described in this study

Taxon	Specimen	Locality/Stratigraphy	Osteoderm morphology
Chroniosuchus lichareví	FG 612/1 FG 612/2 FG 612/3	Gorokhovets, European Russia/Upper Vyatkian Substage, Tatarian Series, Lopingian	Width/axial length >2.5, pitted dorsal ornamentation
Chroniosaurus dongusensis	FG 612/4* FG 612/5	Dongus-6, European Russia; Upper Severodvinian Substage, Tatarian Series, Lopingian	Width/axial length >2.5, pustular dorsal ornamentation
	FG 612/6* FG 612/7	Poteryakha-2, (same data as for locality Dongus-6)	
cf. *Uralerpeton tverdochlebovae*	FG 612/8 FG 612/9	Vyazniki-2, European Russia, Upper Vyatkian Substage, Tatarian Series, Lopingian	Width/axial length <2.5, pitted dorsal ornamentation, small posterodorsal facets
Madygenerpeton pustulatus	FG 596/V/12 FG 596/V/13	Madygen, SW Kyrgyzstan, Madygen Fm, Middle- Late Triassic	Width/axial length >4, pustular dorsal ornamentation, enlarged posterodorsal facets with concentric grooves/ridges

The asterisk signifies specimens of half-moon shaped anterior-end osteoderms.

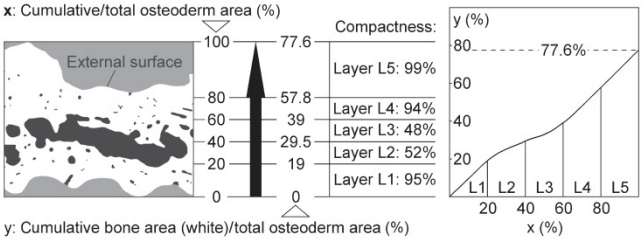

Fig. 3—Digitalisation image of a 5-mm-wide measurement section of *Madygenerpeton pustulatus* osteoderm FG 596/V/12 and the procedure of deriving compactness parameters (L1 to L5, total compactness) and a cumulative compactness curve (on the right). Colours: white, bone area; black, internal space; grey, area outside osteoderm.

south-west outcrop area (environs of the village Madygen) of the late Middle or early Late Triassic Madygen Formation, Batken Region, south-west Kyrgyzstan, Central Asia.

For the comparison of bone compactness profiles, we include further osteoderm thin sections from the material of Witzmann and Soler-Gijón (2010): of the bystrowianid chroniosuchian *Bystrowiella schumanni* the osteoderm specimen SMNS 91226 (sectioned transversally and parasagittally) from the upper Middle Triassic (Ladinian, Upper Lower Keuper) of Vellberg-Eschenau in southern Germany; of the dissorophid temnospondyl *Aspidosaurus* sp. one osteoderm (sectioned parasagittally) belonging to the MCZ 1477 material from the Lower Permian of Texas, Rattlesnake Canyon locality, Nocona Formation, USA; and of the plagiosaurid temnospondyl *P. pustuliferus* the osteoderm specimen SMNS 91227 (sectioned transversally) from the Erfurt Formation, Middle Triassic (Ladinian) of Thuringia, Germany. Furthermore, a transversal thin section of SMNS 91330, a dorsal osteoderm of the plagiosaurid *Gerrothorax* sp. from the upper Middle Triassic (Untere Graue Mergel, Ladinian) of Kupferzell-Bauersbach in southern Germany, was included.

Methods

The dermal bone fragments were embedded in synthetic resin. To cover differences within the histology of the morphologically complex osteoderms the samples were cut either parasagittally (with varying distances from the midline), transversally, or in both directions (see Fig. 2B–F). Polished thin sections with a thickness between 40 and 50 μm were prepared. We were using Leica DC 300 and Zeiss Axiolab A polarisation microscopes for the examination of the thin sections. Besides individual photomicrographs of important details, overview images of the complete sections with a 63- to 80-fold magnification have been generated as mosaics of micrographs (see Fig. 2G–J) by means of a Zeiss Discovery V12 stereomicroscope and an AxioCamMRC5 digital camera system. The latter performs an automatic scan of the thin section in a raster predefined via the device-controlling software AxioVision (module 'MosaiX').

To assess the amount of internal space of the fossil osteoderm bone, which is usually filled with fine sediment, carbonatic, silicic or iron oxide cements, and its distribution over the osteoderm thickness, 5-mm-wide dorsoventral sections of well-preserved osteoderm parts have been demarcated in the overview images. Thereby, posterodorsal facet regions and the close vicinity of the *processus ventralis* have not been considered. Employing a vector graphics software (e.g. CorelDraw), the areas not belonging to the osteoderm and all non-diagenetic internal spaces within the dorsoventrally oriented rectangular demarcation areas have been digitalised as polygons (Fig. 3). In the next step, the demarcation rectangles with (1) osteoderm/outside-osteoderm areas and (2) bone/-non-bone areas marked as black polygons/white background have been transferred to raster images (e.g. TIFF bitmap files). The raster images allow us a simple counting of black and white pixels per line of the raster. Thus, each line of pixels perpendicular to the dorsoventral trend can be assigned a ratio of bone area to overall osteoderm area, i.e. a compactness value. We are parting the dorsoventral sections in one per cent area increments and define the compactness for each increment on the basis of the black-and-white raster data (Supporting information).

Averaging the incremental compactness values over the length of the dorsoventral transect total values of compactness have been derived for each of the 31 measured 5-mm wide dorsoventral sections. Spatial variation of compactness is illustrated by plots of the cumulative percentage of bone area against the cumulative percentage of osteoderm area and by average compactness values for layers of 20 area per cent (L1 to L5 in Fig. 3). These data have been used as a comparison criterion.

Description

We describe the bone histology employing the terminology of Francillon-Vieillot *et al.* (1990). As in the approaches of Scheyer and Anquetin (2008) on turtle shell bone histology and Witzmann and Soler-Gijón (2010) on temnospondyl scutes, we are using the term 'external' for the outer osteoderm section and for the osteoderm surface oriented towards the body surface and 'internal' for the inner section and for the osteoderm surface oriented towards the visceral surface of the body. As our sample only includes dorsal osteoderms, 'external' and

'dorsal' as well as 'internal' and 'ventral' are mostly corresponding. Chroniosuchian osteoderms display a diploë structure, i.e. they comprise compact external and internal cortices with a cancellous region in the middle, which is referred to as the 'interior' here. Following Witzmann and Soler-Gijón (2010), the tubercles and ridges of the external ornament that are cut in the thin sections have been designated as 'saddles' while the grooves and pits between them are referred to as 'valleys'.

External cortex

In most of the specimens, the external cortex consists of homogenous parallel-fibred primary bone and is sparsely vascularised (Fig. 4A,B,E,F), comprising primary vascular channels in low density and more rarely isolated secondary osteons. Osteoderms of cf. *Uralerpeton* have an external cortex made up of less well ordered parallel-fibred bone with a coarse appearance (*sensu* Scheyer and Anquetin 2008) and an inhomogeneous patchy or bundle-wise extinction under cross-polarised light (Fig. 4C). The external cortex is mostly thicker than the internal cortex but not as thick as the cancellous middle region. Often, the thickness varies because of the high relief of the dorsal ornamentation which includes particularly pronounced parasagittal ridges in *Chroniosaurus* and *Madygenerpeton* (see Fig. 2A,H). Exposing the channels and cavities of the middle layer below, a few large and deep incisions occur in the otherwise thick external cortex of the cf. *Uralerpeton* specimens FG 612/8 and 9.

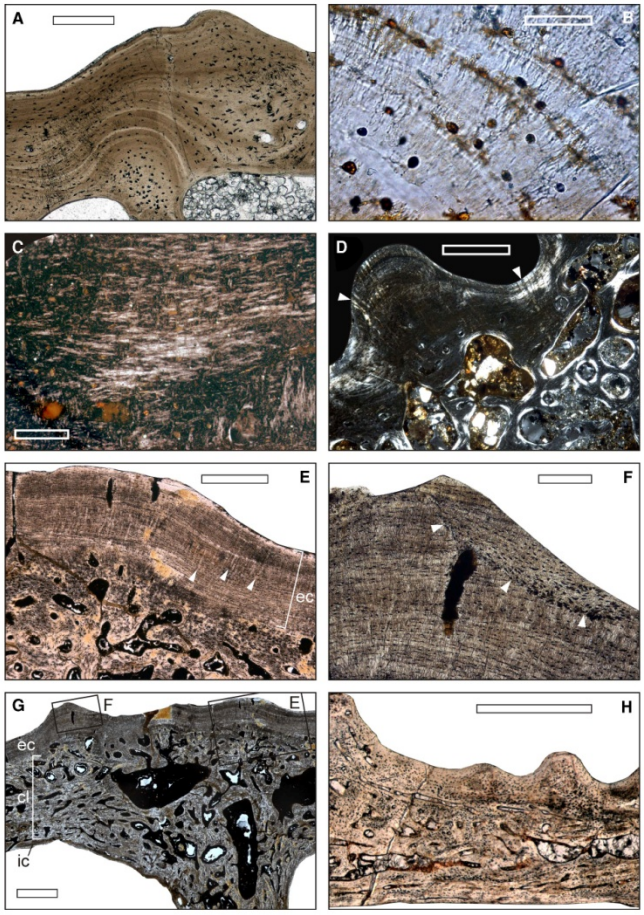

Fig. 4—Chroniosuchid osteoderms: structure of the external cortex (**A**–**F**) and cancellous middle region (**D, E, G, H**). —**A**. *Chroniosaurus dongusensis* specimen FG 612/6, growth zonation and bone cell distribution. —**B**. *Madygenerpeton pustulatus*, specimen FG 596/V/12, growth marks and cell lacunae with long and branched canaliculi. —**C, D**. cf. *Uralerpeton tverdochlebovae*, specimen FG 612/8 in cross-polarised light. Arrows in C mark Sharpey's fibres below sculptural saddles and valleys. Coarse parallel-fibred cortical bone brings about the patchy extinction in **D**. —**E**–**G**. *Chroniosuchus licharevi*, specimen FG 612/1. In E, arrows mark the trend of Sharpey's fibres; in **F**, secondary bone fills the relief of an abraded sculptural saddle (arrows). Large polygonal and smaller shred-like cavities structure the cancellous layer in **G**. —**H**. *Chroniosaurus dongusensis*, transversal section through specimen FG 612/4 with secondary osteons and larger erosion cavities in the middle region. Scale bars: A, F, 0.2 mm; B, 0.05 mm; C, 0.1 mm; D, E, 0.5 mm; G, H, 1 mm.

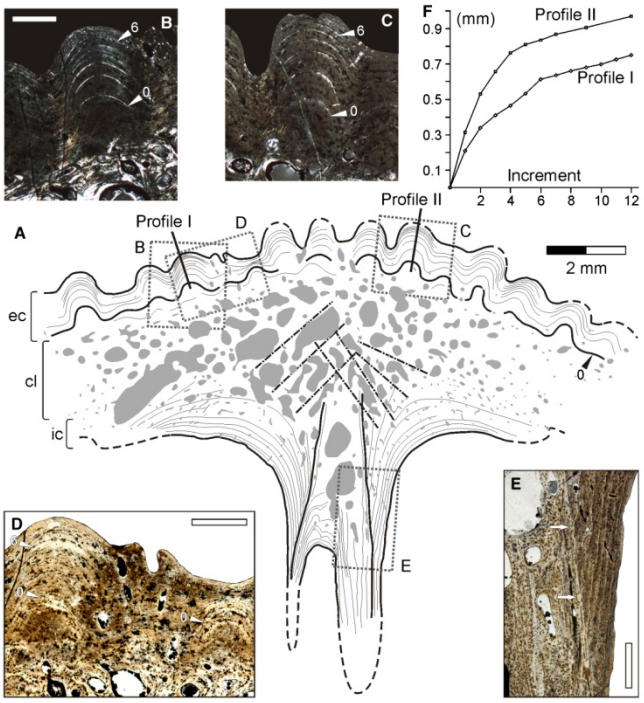

Fig. 5—*Madygenerpeton pustulatus*, specimen FG 696/V/12: Growth zonation, lines of arrested growth and structure of the cancellous layer in the medial part of the osteoderm. —**A**. Schematic drawing of a transversally orientated thin section. Black lines in the external cortex represent resting lines; in the internal cortex they represent growth marks (including resting lines). The dash-dotted lines exemplarily trace the oblique trend of bone trabeculae. Dotted frames indicate the position of detail photomicrographs B–E. —**B, C**. Detail photomicrographs of the external cortex in cross-polarised light. —**D, E.** Detail photomicrographs in normal light. —**F**. Growth profiles for two transects through the external cortex with relatively complete preservation of LAGs. Arrows with number in A–D mark lines of arrested growth (numbering consistent with diagram in F); arrows in E point to the tapering of younger resting lines at an older resting line. Unlabelled scale bars: 0.5 mm.

The external cortex of chroniosuchids is marked by a high density of cell lacunae which have long and branched canaliculi in *Chroniosuchus*, cf. *Uralerpeton* and *Madygenerpeton* (Fig. 4B) In *Chroniosuchus* and *Madygenerpeton*, shape and arrangement of the lacunae and canaliculi are often following the direction of bone fibres and bone growth marks. No regular variation in the orientation of lacunae and canaliculi occurs in cf. *Uralerpeton*, and in the *Chroniosaurus* sample the external cortices are marked by lacunae in irregular arrangement with short or no canaliculi.

The studied chroniosuchid specimens feature growth marks in the external cortex that are often well visible under normal light (Figs 4A,B,E,F and 6C). They reflect modifications of the sculptural relief during the preserved growth phase of the cortex. Especially in osteoderms with pustular ornamentation, relief compensation and buried saddles occur frequently (Figs 4A, 5A and 6C), whereas in *Chroniosuchus licharevi*, the position of sculptural maxima appears to be relatively constant over time. Both of the sectioned *Madygenerpeton* specimens display a dense growth zonation and some of the bone growth marks, that are also visible in cross-polarised light as thin and light horizons within the otherwise homogenous parallel-fibred bone, apparently represent lines of arrested growth (LAGs, resting lines *sensu* Francillon-Vieillot *et al.* 1990), (Fig. 5). In some of the sculptural saddles that are only moderately overprinted with iron oxide cements, the presumable lines of arrested growth are preserved in a complete profile, documenting variation in growth increment width (Fig. 5F, Supporting information). Apart from bone growth marks, the primary bone of external cortex in cf. *Uralerpeton* is structured by undulating cementing lines that may represent lines of bone resorption. Sculptural saddles in *Chroniosuchus* specimen FG 612/1 display a marked concave boundary line between primary parallel-fibred bone and equally compact secondary bone filling the relief (Fig. 4F), indicating bone re-growth after either resorption or abrasion through an injury.

Sharpey's fibres, i.e. mineralised ingrowing fibrillary processes from adjacent soft tissues (Francillon-Vieillot *et al.* 1990, p. 504), occur in the external cortices of all osteoderm samples and are sometimes also visible in normal light (Fig. 4E). In *Chroniosuchus* and cf. *Uralerpeton*, they appear to be more abundant below the saddles of the dorsal sculpture than below the valleys (Fig. 4D). Sometimes they reach their highest density along the saddle flanks and not at the top (see Fig. 7A). In the external cortices of the sculptured osteoderm parts of *Chroniosaurus* and *Madygenerpeton*, Sharpey's fibres are notably less abundant than in the external cortex of

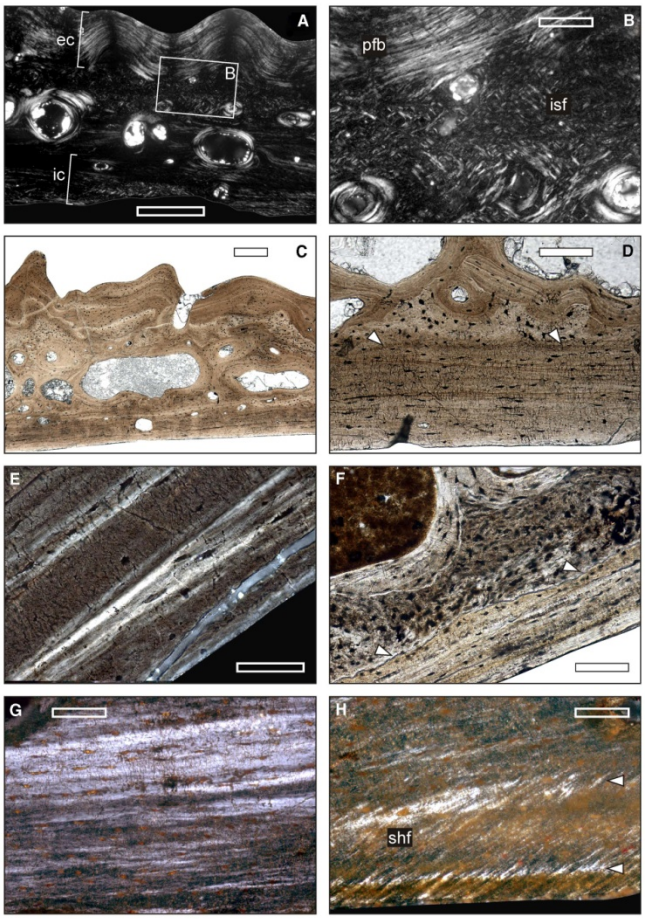

Fig. 6—Chroniosuchid osteoderms: structure of the middle layer (A–C) and internal cortex (D–H). —**A**, **B**. *Chroniosaurus dongusensis*, specimen FG 612/7 in cross-polarised light. —**C**–**E**. *Chroniosaurus dongusensis*, specimen FG 612/6. Arrows in D mark the boundary between the middle region and more orderly zonal bone of the internal cortex. In cross-polarised light (E) domains of contrasting extinction indicate the transition of parallel-fibred to lamellar cortical bone. —**F**. cf. *Uralerpeton tverdochlebovae*, specimen FG 612/8. Arrows mark the undulating boundary between osteoderm middle region and internal cortex. —**G**, **H**. *Chroniosuchus licharevi*, specimen FG 612/2 in cross-polarised light. The parallel-fibred primary bone in G is marked by local transitions to lamellar bone. Sharpey's fibres in H are dense, contacting the internal osteoderm boundary in a low acute angle. Scale bars: A, C, 0.5 mm; B, D, F–H, 0.1 mm; E, 0.05 mm.

Chroniosuchus osteoderms and the density of such fibres is higher below valleys of the dorsal ornamentation than at the saddle tops.

Middle region

The structure of the osteoderm middle region is variable among the sampled chroniosuchid taxa (see Table 2). Mostly its thickness accounts for approximately 50% of the total thickness, but it can constitute up to 70% in *Chroniosuchus* (Figs 4G and 7A) and cf. *Uralerpeton* or <40% in the *Chroniosaurus* osteoderms (Fig. 6A,C). In *Chroniosuchus*, the thickness of the cancellous layer depends on the dorsal ornamentation relief, i.e. it is extended below sculptural saddles. With the exception of some *Chroniosaurus* sections (see Fig. 6A), the degree of remodelling is high, as indicated by voluminous erosive cavities, and only minor areas of parallel-fibred primary bone (Figs 4G, 5A, 6C, 7A, and 8).

In the Poteryakha-2 specimens of *Chroniosaurus*, the unaltered primary bone matrix accounts for a relatively high amount of the total volume. Well separable from the homogenous parallel-fibred bone of the external cortex in cross-polarised light, the bone matrix of the osteoderm middle region of these specimens is either structured by distinct fibre bundles of coarse parallel-fibred bone or by networks of overcrossing collagen fibres alternating with zones of parallel-fibred bone (in FG 612/7; Fig. 6A,B). These fibre networks appear to represent 'interwoven structural fibres' similar to those described for osteoderms of the *Plagiosuchus pustuliferus* and *Bystrowiella schumanni* (Witzmann and Soler-Gijón 2010),

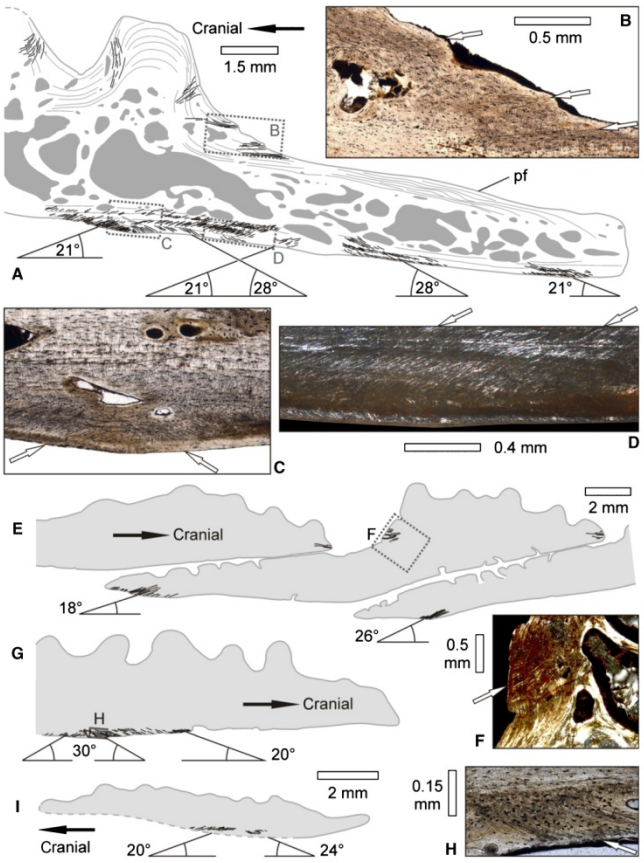

Fig. 7—Sharpey's fibres within the internal cortex and close to the facet areas. —**A**–**D**. *Chroniosuchus licharevi*, specimen FG 612/2: A, schematic drawing; B, C, detail photomicrographs of the internal and external cortices in normal light; D, detail photomicrograph of the internal cortex in cross-polarised light. —**E**, **F**. Schematic drawing and detail photomicrograph of *Madygenerpeton pustulatus*, specimen FG 596/V/13. —**G**, **H**. Schematic drawing and detail photomicrograph of cf. *Uralerpeton tverdochlebovae* specimen FG 612/8. —**I**. Schematic drawing of *Chroniosaurus dongusensis*, specimen FG 612/7. All depicted thin sections have a parasagittal orientation. White arrows and angle diagrams indicate the trend of Sharpey's fibres (black lines). Dotted rectangular frames designate the position of B–D, F, and H.

anurans (Ruibal and Shoemaker 1984) and various amniote groups (e.g. Scheyer and Sander 2004; Main *et al.* 2005; Hill 2006; Scheyer and Sánchez-Villagra 2007; Scheyer and Anquetin 2008; Vickaryous and Hall 2008). Osteoderm sections displaying structural fibres are marked by irregularly arranged lacunae without canaliculi.

The compactness of the middle region varies with the shape and size of the erosive cavities and often it increases at the lateral, anterior and posterior ends. In *Chroniosuchus* and cf. *Uralerpeton*, the middle region is dominated by large cavities that have a polygonal shape and are separated by only thin trabeculae of secondary bone. Medially, the interior of *Chroniosuchus* osteoderms comprises a central layer of large polygonal cavities surrounded by more dense secondary bone tissue with numerous smaller elongated and irregularly branching cavities (see FG 612/1, Fig. 4G). *Chroniosaurus* and *Madygenerpeton* are marked by erosive cavities that have rather roundish than polygonal outlines and are not as dense as in *Chroniosuchus* and cf. *Uralerpeton* (see Figs 6A,C and 8). Among the *Chroniosaurus* specimens, the osteoderm samples from Dongus-6 (FG 612/4 and 5; see Fig. 4H) display a cancellous layer with lower amounts of primary bone and more channel-like transversally oriented cavities than osteoderms from Poteryakha-2, whose isometric cavities are lined with thick secondary bone (FG 612/6 and 7, Fig. 6A–D). Between anterior-end and trunk osteoderms of *Chroniosaurus*, the overall compactness may differ slightly but no marked dissimilarity occurs.

Internal cortex

The internal cortex usually forms the thinnest layer of a chroniosuchid osteoderm and may locally taper off. In most specimens, it consists of homogenous or coarse parallel-fibred

Table 2 Variation in the osteoderm microstructure of four studied chroniosuchid taxa and the bystrowianid *Bystrowiella schumanni* (from Witzmann and Soler-Gijón 2010, p. 99-101). The asterisk marks terms that describe differences in compactness according to the scheme of Francillon-Vieillot *et al.* (1990)

	Primary bone matrix			
Taxon	ec	mid region	ic	Structure of the osteoderm middle region
Chroniosuchus	pfb	pfb	pfb - lb	Highly remodelled, trabecular to coarse cancellous*
Chroniosaurus	pfb	(c)pfb + isf	pfb - lb	Moderately to highly remodelled, coarse cancellous*
cf. *Uralerpeton*	cpfb	cpfb	cpfb	Highly remodelled, trabecular*
Madygenerpeton	pfb	pfb	pfb	Highly remodelled, coarse cancellous*
Bystrowiella	pfb	isf	pfb	Lowly remodelled, fine cancellous*

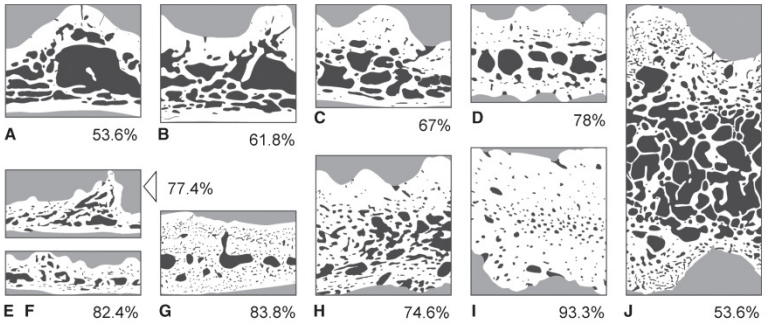

Fig. 8—Amount and distribution of internal space in exemplary compactness measurement sections (5 mm width) of all sampled taxa (see Fig. 2, Supporting information). —**A**, **B**. *Chroniosuchus licharevi*, sections FG 612/3-t and 2-t-1. —**C**. cf. *Uralerpeton tverdochlebovae*, section FG 612/8-t-2. —**D**. *Madygenerpeton pustulatus*, section FG 596/V/12-t-1. —**E**, **F**. *Chroniosaurus dongusensis*, sections FG 612/5-t-3 and 5-t-2; **G**, *Bystrowiella schumanni*, section SMNS 91226-t-1. —**H**. *Gerrothorax* sp., section SMNS 91330-t-1. —**I**. *Plagiosuchus pustuliferus*, section SMNS 91327-t. —**J**, *Aspidosaurus* sp., MCZ 1477-p-1.

primary bone. The internal cortex may have a more orderly structure than the primary bone matrix of the contacting layer of the osteoderm middle region (Fig. 6D,F). Some osteoderm sections of *Chroniosuchus* and *Chroniosaurus* feature homogenous parallel-fibred bone with local transitions to lamellar bone which are indicated by contrasting zone-wise extinction in cross-polarised light (Fig. 6E,G). The oval or roundish shape of bone cell lacunae in successive layers of this bone type reflects the corresponding change of cell and fibre orientations in successive zones of contrasting extinction (see Fig. 6E; Francillon-Vieillot *et al.* 1990).

In chroniosuchid osteoderms, the internal cortex is avascular to moderately interspersed by primary vascular channels, mostly in accordance with the degree of vascularisation in the external cortex. Growth zonations in the internal cortex are common and often as defined (see Fig. 6D,F), but may be of lower contrast than in the external cortex. In *Madygenerpeton*, lines of arrested growth are rare and only barely recognisable in cross-polarised light despite a very pronounced pattern of growth marks which probably was to some degree synchronous to the resting lines in the external cortex.

Only in four parasagittal thin sections which were cut close to the dorsal midline, Sharpey's fibres have been found within the internal cortex. In cross-polarised light the parasagittal sections of FG 612/2, 612/7, 612/8, and FG 596/V/13 (representing each of the four considered chroniosuchid taxa) display dense bundles of thin fibres running oblique to the zonation of the parallel-fibred cortical bone (Figs 6H and 7). In FG 612/2 and 612/8, these fibres are also visible in normal light (Fig. 7B,C,H). Unlike the more variable configuration in the external cortex, the fibre orientation within a bundle of Sharpey's fibres in the internal cortex displays only minor variation (see Figs 6H and 7). The fibre bundles only occur in the posterior non-overlapping part of the inner cortex and display a posteroventral trend in FG 596/V/13 and both, anteroventral and posteroventral trends in FG 612/2, 7, and 8 (see Fig. 7A). Mostly the Sharpey's fibres are dipping shallowly at angles between 20° and 30° towards the internal osteoderm boundary. Whereas in the specimens, FG 612/7 and 8 one

posterior bundle of posteroventral fibres and one anterior bundle of anteroventral fibres are preserved, the *Chroniosuchus* specimen FG 612/2 features several bundles with alternating orientations (see Fig. 7A,C,G,I). The contrasting orientations of Sharpey's fibres close to the internal osteoderm boundary and close to the osteoderm middle region leads to a conspicuous herring-bone pattern in one part of the internal cortex of FG 612/2.

Central body and ventral process

Chroniosuchid osteoderms are marked by a medial to lateral differentiation in morphology and osteohistology. In the transversal sections of FG 612/1, 4, 5, and 7 as well as FG 596/V/12, a characteristic edge on the internal surface and an associated bend in the parallel-fibred bone of the internal cortex mark the boundary line between the lateral osteoderm wings and the osteoderm central body (*corpus scuti dumi*) that forms a prominent plateau from which the ventral process as well as to the anterior wings and posterior processes arise (see Figs 5A and 11).

In the transversal sections of *Chroniosuchus* specimen FG 612/1 and *Madygenerpeton* specimen FG 596/V/12, the thickness of the cancellous middle region considerably increases towards the medial plane, enlarging the contact zone between the main plate of the osteoderm (i.e. the platy part parallel to the dorsal body surface) and the midsagittal ventral process (Fig. 5A). In FG 596/V/12 the internal cortex also contributes much to the medial thickening. It features an increased density of primary vascular channels – as in the medial part of some *Chroniosaurus* osteoderms – and wide-spaced bone growth marks that end unconformably at older growth marks of the ventral process (Fig. 5E). Both osteoderms, FG 612/1 and FG 596/V/12, display medially a layer of lowest compactness that is further away from the internal osteoderm surface than in the lateral osteoderm sections. The medial contact zone of the ventral process is marked by a ventrolateral trend of trabeculae in the cancellous layer (oblique to the main plate and ventral process of the osteoderm (Fig. 5A: dash-dotted lines; see also Fig. 4G).

Similar to the lateral wings of the osteoderm, the ventral process has a diploë structure with a cancellous interior and cortices which form a seamless connection to the internal cortex of the central osteoderm body. In *Madygenerpeton* specimen FG 596/V/12, the asymmetrical pocket-like incision of the ventral process that encloses the neural spine of the adjacent vertebrae is preserved (Fig. 5A). As the growth mark pattern around the incision demonstrate, the distance between vertebra and main plate of the osteoderm was not static but changed during the ontogenesis.

Facet areas

Unlike the external cortex in the ornamented part of the chroniosuchian osteoderms, the thinner external cortices below the posterodorsal articulation facets are devoid of Sharpey's fibres in all considered specimens. With the exception of the *Madygenerpeton* osteoderms, the degree of vascularisation of the cortex is similar to that of the ornamented sections. In the *Madygenerpeton* specimens, numerous primary vascular channels end on the facets which appear to be pockmarked by roundish foramina (denoted for specimen FG 596/V/13 in Fig. 7E). The foramina often occur within the grooves of the groove-and-ridge-system relief which is characteristic for the articulation facets of *Madygenerpeton* osteoderms (Schoch *et al.* 2010).

The rear sides of the dorsal sculptured areas immediately adjoining the posterodorsal facet areas of *Chroniosuchus* specimen FG 612/2 and *Madygenerpeton* specimen FG 596/V/13 display thin distinct bundles of Sharpey's fibres with a conspicuous posterior trend (Fig. 7A,B,E,F). In FG 696/V/13, corresponding bundles of anteriorly trending peripheral fibres occur at the anterior osteoderm margin.

A pair of anteroventral facets constitutes the contact zone of the posteriorly following osteoderm towards the posterodorsal facets of its anterior neighbour. Similar to the state of the external cortex below facet regions, Sharpey's fibres are generally lacking for the overlapping zones of the internal cortex. Whereas the anteroventral facets are morphologically indistinct from the rest of the internal surface in other chroniosuchids, those of *Madygenerpeton* reproduce mirror-inverted groove and ridge pattern of the posterodorsal facets and display similar foramina (see Buchwitz and Voigt 2010, figs 2, 3).

Results of the compactness analysis

The compactness of 31 measured sections varies between 51.8% and 93.3%. The values for chroniosuchians appear to be continuously distributed over the whole spectrum and their compactness profiles overlap with both, the dissorophid and the plagiosaurid sample (Table 3; Figs 8 and 9A). While compactness profiles of *Bystrowiella*, *Chroniosaurus*, and *Madygenerpeton* osteoderms are closer to those of plagiosaurids, profiles of *Chroniosuchus* and cf. *Uralerpeton* sections show more similarity to those of the dissorophid *Aspidosaurus* (Fig. 9A,B).

Most often the compactness values of the five successive 20%-thickness layers (L1 to L5 in Fig. 4) are correlated or highly correlated with each other and with the overall compactness of the measured sections (Table 4). The compactness of the external-most 20% layer (L5), however, is only poorly correlated with other compactness measures. In particular, its correlation with the compactness of the second fifth (L2) is low. Plotting the compactness ratio of L2 and L5 against the overall compactness, a difference in the distribution of internal space between chroniosuchid sections and other measured osteoderms is revealed (Fig. 9C): Among osteoderm sections with a similar total amount of compactness, the chroniosuchid sections display a compactness ratio

Table 3 Results of the compactness measurements: Overall compactness values ('total') and compactness of layers L1 to L5 for all considered taxa. The number of measured sections/osteoderms is listed in column '*n*'

		Compactness [%]					
Taxon	*n*	L1	L2	L3	L4	L5	Total
Temnospondyli	7/3	71–91	35–93	21–90	44–96	74–97	54–93
Aspidosaurus	3/1	71–80	35–50	21–30	44–56	74–85	54–56
Gerrothorax	3/1	70–88	62–69	50–77	83–92	91–97	75–83
Plagiosuchus	1/1	91	93	90	96	96	93
Chroniosuchia	24/10	70–99	7–97	19–90	49–96	81–99	52–93
Bystrowiella	3/1	93–99	76–97	66–90	88–94	93–95	83–93
Chroniosuchidae	21/9	70–99	7–74	19–75	49–96	81–99	52–85
Chroniosuchus	5/3	72–87	7–62	20–36	57–73	81–98	53–68
Chroniosaurus	5/2	89–99	60–74	63–72	79–91	85–97	77–85
cf. *Uralerpeton*	6/2	70–92	25–52	19–63	49–82	95–98	52–74
Madygenerpeton	5/2	90–96	44–60	48–75	61–96	96–99	72–85

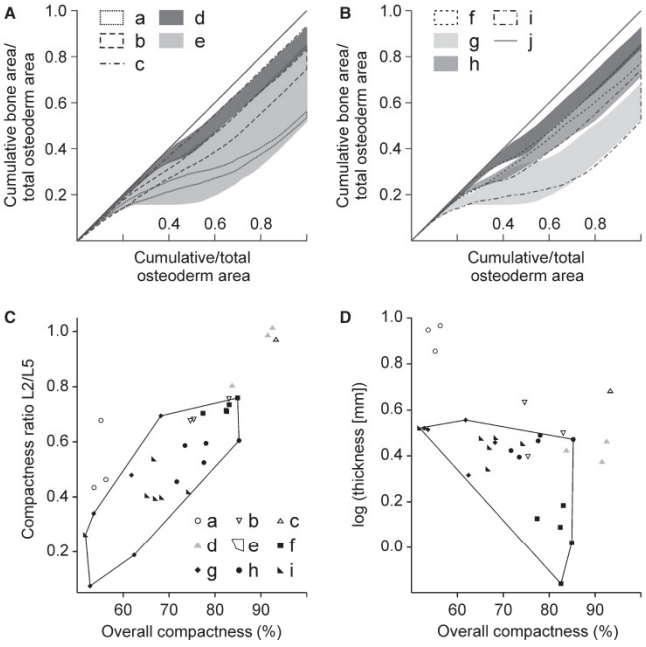

Fig. 9—Results of compactness analysis. —**A, B**. Cumulative compactness plots. —**C**. Compactness ratio of 20%-layers L2 and L5 plotted against overall compactness. —**D**. Logarithm of section thickness plotted against overall compactness. Labels: a, *Aspidosaurus* sp.; b, *Gerrothorax* sp.; c, *Plagiosuchus pustulifer-us*; d, *Bystrowiella schumanni*; e, Chroniosuchidae (convex hull of associated data points in C, D); f, *Chroniosaurus dongusensis*; g, *Chroniosuchus licharevi*; h, *Madygenerpeton pustulatus*; i, cf. *Uralerpeton tverdochlebovae*; j, line of 100 per cent compactness.

which is mostly lower. Furthermore, there appears to be a dependence of thickness and compactness as a consequence of the markedly deviant thicknesses of the *Aspidosaurus* and *Chroniosaurus* samples (Fig. 9D).

Discussion

Homology of the chroniosuchian osteoderms

The assumption that dorsal osteoderms of the two principal chroniosuchian groups, Bystrowianidae and Chroniosuchidae, are homologous structures was questioned by Golubev (1998) who considered the overlap of the posterodorsal osteoderms facets in chroniosuchids by a posteriorly following osteoderm as antithetic to the overlap of the broad dorsal facets on the anterior wings of bystrowianid osteoderms (see *Bystrowiella* in Fig. 10A) by an anteriorly following osteoderm. He argued that this disparity in morphology and arrangement contradicted the hypothesis of their homology (Golubev 1998; p. 280). Novikov and Shishkin (2000), however, proposed a homology hypothesis that could solve this paradox: Assuming that bystrowianid osteoderms correspond only to

Table 4 Correlation matrix for compactness values of the 20% thickness layers L1- L5 and total compactness. In the lower left half, correlation coefficients for the chroniosuchid sample (n = 21) are listed; upper right half: values for the complete sample (n = 31)

	L1	L2	L3	L4	L5	Total
L1	–	0.525	0.686	0.691	0.350	0.800
L2	0.701	–	0.813	0.662	0.152	0.885
L3	0.745	0.815	–	0.770	0.378	0.941
L4	0.761	0.652	0.627	–	0.506	0.885
L5	0.278	0.042	0.127	0.215	–	0.455
Total	0.869	0.911	0.924	0.846	0.228	–

the central body of chroniosuchid osteoderms, the peg-like anterior processes of chroniosuchids (see Fig. 2A) may be homologous to the platy anterior wings of bystrowianids (further congruencies in Novikov and Shishkin 2000, p. 168). An independent test of this kind of morphology-based homology hypothesis is provided by the comparison of histological characteristics of the two osteoderm types.

The only yet considered sample of the bystrowianid *Bystrowiella* (specimen SMNS 91226; Witzmann and Soler-Gijón 2010) differs markedly in its histology from the chroniosuchid osteoderms described in this study (see Fig. 10A): Whereas the interior of chroniosuchid osteoderms is of low compactness, featuring large erosive cavities lined with secondary bone and only minor areas of parallel-fibred primary bone, the middle region of the *Bystrowiella* osteoderm is dominated by a homogenous primary bone matrix with a regular pattern of interwoven structural fibres. The cancellous layer accounts for less than one forth in *Bystrowiella* and divides the osteoderm symmetrically (Fig. 10B,C) – unlike the state in chroniosuchids, whose thick cancellous layer separates the thin internal and relatively thick external cortices. In chroniosuchids, Sharpey's fibres are not only abundant in the external cortex, but also occur as distinct bundles in the internal cortex. Featuring

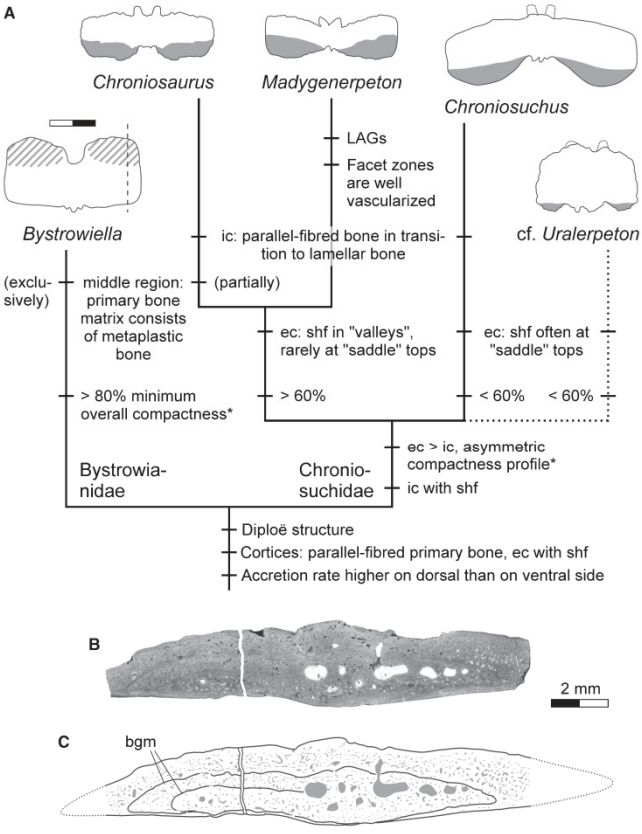

Fig. 10—Osteoderm histology of *Bystrowiella schumanni* compared to that of chroniosuchids. —**A**. Tree diagram for the Chroniosuchia; topology modified from Schoch *et al.* (2010). *Bystrowiella* and cf. *Uralerpeton* have been incorporated on the basis of the assumption that Chroniosuchidae is a monophyletic group. The asterisk marks characters based on the compactness analysis of 5-mm-wide dorsoventral transects (see Figs 3, 8 and 9). Posterodorsal facets are grey-shaded; the lined areas indicate the position of facets on the anterior wings of *Bystrowiella* (after Witzmann *et al.* 2008). The dashed line marks the position of the thin section depicted below. —**B**, **C.** *Bystrowiella schumanni*, parasagittal section through specimen SMNS 91226 displaying growth marks (black lines) that indicate a high dorsal and low ventral accretion of bone throughout the preserved part of the ontogenesis. Cavities and vascular channels are grey-shaded. Note that the central position of the cancellous layer is not concordant with the pattern of growth marks.

a high overall compactness, domains of interwoven structural fibres and often an only moderately remodelled middle region the osteoderm samples of *Chroniosaurus* display the highest similarity with the *Bystrowiella* specimen. As no bystrowianid osteoderms have been studied histologically apart from this one specimen, conclusions regarding the distinctness of bystrowianid osteoderm histology have to be treated with caution. In view of all mentioned aspects, the hypothesis that chroniosuchid and bystrowianid osteoderms are homologous skin derivatives cannot be rejected on the basis of present histological data.

Mode of skeletogenesis

The bone microstructures of chroniosuchian osteoderms indicate similar modes of skeletogenesis as in the dermal bone types of other crown-group tetrapods: Ossification via metaplasia in *Bystrowiella* and some of the *Chroniosaurus* specimens can be inferred from the presence of interwoven structural fibres, i.e. remnants of the former dense dermal or connective tissues that were transformed into dermal bone (see Scheyer and Sander 2004), and from absence of canaliculi in the bone cell lacunae (see Haines and Mohuiddin 1968; Main *et al.* 2005). Osteoderms that formed partially by metaplasia also occur in the plagiosaurid temnospondyl *Plagiosuchus* (Witzmann and Soler-Gijón 2010), anurans (Ruibal and Shoemaker 1984), squamates (Zylberberg and Castanet 1985; Levrat-Calviac and Zylberberg 1986), crocodylians (Vickaryous and Hall 2008), dinosaurs (e.g. de Ricqlès *et al.* 2001; Scheyer and Sander 2004; Main *et al.* 2005; Cerda and Powell 2010) and some xenarthrans (Hill 2006). Often, metaplastic primary bone does not form the outermost layer but it is enclosed in periosteal bone. As in the *Chroniosaurus* osteoderms from the locality Poteryakha-2, which comprise domains of metaplastic bone within a primary bone matrix dominated by parallel-fibred bone, intermediate states between metaplastic bone and periosteal bone have also been observed within dermal bones of other basal tetrapods and reptiles (e.g. Main *et al.* 2005; Scheyer and Sánchez-Villagra 2007; Witzmann 2009; Witzmann and Soler-Gijón 2010). Lacking interwoven structural fibres, most of the sampled chroniosuchian osteoderms comprise parallel-fibred bone as the only type of primary bone, indicating that they may have formed entirely through intramembraneous ossification similar to the mode of skeletogenesis in the dermal armour of the extant armadillo *Dasypus* (Vickaryous and Hall 2006), pareiasaurs (Scheyer and Sander 2009), placodonts (Scheyer 2007), some temnospondyls (Witzmann and Soler-Gijón 2010) and some aetosaurs (Cerda and Desojo in press).

Similarities in the initial development and microstructure of chroniosuchian osteoderms and those of other tetrapods cannot be explained by simple homology as the dorsal osteodermal shields of chroniosuchians have no equivalent among related stem-group amniotes (see Fig. 1A,B). In fact, with the exception of some microsaur species, which display a minor osteoderm cover in the throat or shoulder girdle region (Carroll and Gaskill 1978), osteoderms appear not to be present at all in other groups of the amniote stem. Thus, we find likely that chroniosuchian osteoderms represent another example for the multiple independent origin of osteoderms within the dermis of tetrapods (see also Ruibal and Shoemaker 1984; Hill 2005; Scheyer and Sander 2009; Witzmann and Soler-Gijón 2010).

Aspects of osteoderm development

The presence of zonal periosteal bone in the cortices of all sampled chroniosuchid osteoderms allows us to infer allometries during the latter part of the ontogenesis. Chroniosuchid osteoderms display a marked difference between internal and external cortices (see Figs 4G,H, 6A,C, 8A–F and 9C): Whereas the external cortex is relatively thick, usually displays a high ornamentation relief and is composed of parallel-fibred bone, the thin internal cortex can show transitions to slower growing lamellar bone as indicated by zones of contrasting extinction in cross-polarised light (Fig. 6E,G). The interpretation that accretion on the inside of the chroniosuchian osteoderm was actually slower than on its outside is in agreement with the higher distinctness of LAGs in the external cortex of *Madygenerpeton* samples and with the structure of circumferentially preserved growth marks in the *Bystrowiella* specimen which demonstrate that at some point of the ontogenesis the growth on the inside of the osteoderm came almost to a rest and only the external cortex grew further (Fig. 10B,C).

Whereas the thin *Chroniosaurus* osteoderms display a T-shape when sectioned transversally, the thicker osteoderms of *Madygenerpeton* and *Chroniosuchus*, which belonged to larger individuals, display an increased thickening in the contact region between the horizontal plate of the osteoderm and the ventral process. Wide-spaced growth marks and a higher density of primary vascular channels in the internal cortex of *Madygenerpeton* indicate that its medial thickening is in fact reached by higher growth rates of the internal cortex (see Fig. 5A). In *Chroniosuchus*, the internal cortex close to the ventral process was probably growing faster as well but its late growth phase is obscured by a stronger bone remodelling than in *Madygenerpeton* which resulted in an expansion of the cancellous middle layer at the expense of the internal cortex. Apart from the thickening, the medial cancellous layer in the contact zone to the ventral process of *Madygenerpeton* specimen FG 596/V/12 displays a conspicuous oblique trend of bone trabeculae (Fig. 5A). Probably both the thickening and the orientation of trabeculae strengthened the attachment of the ventral process and increased the loading capacity of the osteoderm. The length of the ventral process which determines the distance between the osteoderm main plate and the transversal processes of the vertebrae is only slightly increasing in specimen FG 596/V/12.

According to a generalised growth scheme for chroniosuchid osteoderms, an initially T-shaped osteoderm, consisting

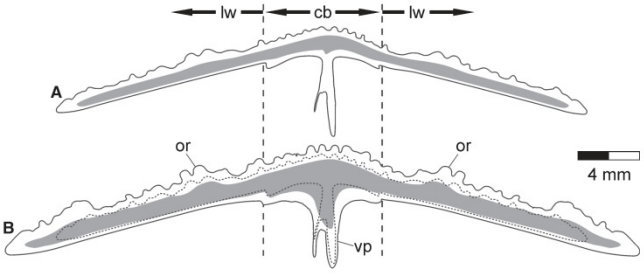

Fig. 11—Osteoderm shape change during the latter part of the ontogeny. —**A**. Schematic transversal section through the dorsal osteoderm of a pre-adult chroniosuchid. —**B.** Transversal osteoderm section for an adult individual (scheme modified from specimen growth series in FG 596/V/12, see Fig. 5). The dashed line represents the earlier osteoderm outline; the cancellous layer is grey-shaded. Scale bar: 4 mm.

of a thin ventral process and a thin and narrow main plate (Fig. 11A), develops by dominating lateral and dorsal accretion, and, after a certain size limit is reached, by thickening of the anchoring of the ventral process (Fig. 11B). Notwithstanding the distance between osteoderm and the vertebral centrum might have changed only slightly given the simultaneous medial thickening of the internal cortex and elongation of the ventral process. The position of parasagittal ornamentation ridges appears to be relatively constant over time and the gradient of the dorsal relief apparently increases with raising osteoderm thickness.

Resting lines within bone cortices of fossil and extant poikilotherm tetrapods are often interpreted as the result of an annual growth cycle and form the basis of skeletochronology (e.g. Peabody 1961; Castanet *et al.* 1993; Scheyer *et al.* 2010). Assuming that resting lines in the osteoderms of *Madygenerpeton* reflect an annual periodicity as well, we infer growth rates and a minimum individual age for specimen FG 596/V/12: The thickest growth increments of its external cortex demonstrate that its maximum growth rate exceeded 0.3 mm per period. If the period was 1 year, this osteoderm would have belonged to an individual that was more than 12 years old. The spacing of increments towards the external surface reflects a continuous decrease in accretion of periosteal bone at the beginning of the recorded time span and during the last 6 years of life accretion occurred at a constant low growth rate (Fig. 5B,C,F). Given this kind of growth profile, we interpret the individual to whom FG 596/V/12 belonged as an adult.

Sharpey's fibres and muscle attachment

Sharpey's fibres in the external cortex of the sculptured osteoderm parts can vary considerably in thickness, abundance and orientation (Fig. 4D–E). They often have perpendicular or high-angle orientations towards the outer osteoderm surface and probably represent anchoring fibres from an overlying dermal connective tissue. To some degree, the distribution patterns of Sharpey's fibres in the external cortex vary between the chroniosuchid species (see Fig. 10A) and may be related to the type of ornamentation. In contrast, Sharpey's fibres in the internal cortex of chroniosuchid osteoderms form strictly localised dense bundles with low variation in the orientation of individual fibres, which run towards the internal boundary of the osteoderm at acute angles of 30° or less (see Fig. 7). Previous studies documented Sharpey's fibres in the internal cortex or basal layer of dorsal osteoderms of various tetrapod groups, such as, squamates (de Buffrénil *et al.* 2010), phytosaurs, crocodylians (Scheyer and Sander 2004; Vickaryous and Hall 2008; Klein *et al.* 2009), thyreophoran dinosaurs (Scheyer and Sander 2004) and temnospondyls (Witzmann and Soler-Gijón 2010). In most groups, these fibres have been interpreted as incorporated tissue of the skin, muscles, tendons or ligaments that effected a more forceful attachment of the osteoderms.

However, such an attachment function cannot explain the patterns of Sharpey's fibres observed in the craniocaudally segmented crocodylian dorsal shields which have the two middle osteoderms of each multi-osteoderm shield segment inflexibly attached to the spinous process of one associated vertebra through an intermediate layer of apical cartilage and cingular ligaments (Frey 1988*a*,*b*; Salisbury and Frey 2000). Two or four osteoderm rows in the middle of the dorsal shield constitute the so-called paravertebral shield which functions as an attachment site for the epaxial musculature. The epaxial muscles systems span several vertebral segments between the transverse processes of the vertebrae and the ventral side of the paravertebral osteoderms. This particular suspension considerably contributes to the support of the trunk during raised gait on land and forms a crucial component of the various trunk constructions in fossil and recent Crocodylia (*sensu* Martin and Benton 2008) referred to as bracing systems (see Frey 1988*b*; Salisbury and Frey 2000; Schwarz-Wings *et al.* 2009).

Apart from crocodylians, dorsal osteoderm systems with a rigid connection to the vertebral column occur as well in dissorophid temnospondyls (Dilkes and Brown 2007; Dilkes 2009), but in the internal cortex of their osteoderms Sharpey's fibres have not been found. Arguably, they are absent because a further soft tissue anchoring of the osteoderms was not required (Witzmann and Soler-Gijón 2010). Chroniosuchids and crocodylians, however, share dense bundles of shallowly dipping Sharpey's fibres in the internal cortex of the shield segments (consisting of one only osteoderm in chroniosuchians)

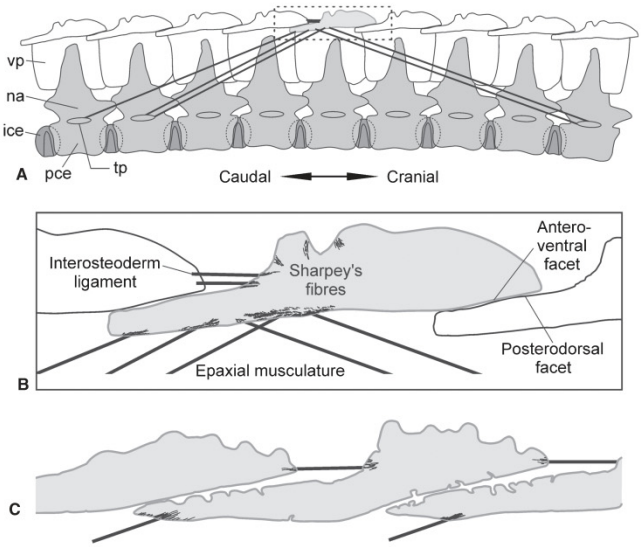

Fig. 12—Schematic reconstruction of epaxial muscle suspension and interosteoderm ligaments in the chroniosuchid trunk. —**A, B**. Reconstruction on the basis of osteoderm specimen FG 612/2 (parasagittal thin section), a ratio of height to segment length of 1.4, and a dorsal curvature of 1° per segment. Vertebral structure and osteoderm contact according to V'yushkov (1957*a*) and Buchwitz and Voigt (2010). —**C**. Orientation of muscles and ligaments for the osteoderms of specimen FG 696/V/13 which has been sectioned more laterally than FG 612/2.

and a stiff or joint-like connection between the shield segments and associated vertebrae (see also Discussion by Clack and Klembara 2009; Buchwitz and Voigt 2010). Our conclusion is that the insertion of the epaxial musculature to the ventral side of chroniosuchian osteoderms evolved convergent to the arrangement in crocodylian bracing systems and was not functionally related to the already sophisticated anchoring of the osteoderms but supported the carrying of the trunk during terrestrial locomotion. In agreement with such an analogy Sharpey's fibres in the internal cortex of chroniosuchian osteoderms have only been documented in parasagittal thin sections cut close to the midsagittal plane and not further laterally (see all documented occurrences in Fig. 7); they do not occur in the zone of anteroventral overlap by the neighbouring osteoderm, and they have an either anteroventral or posteroventral orientation, meeting the osteoderm surface at acute angles smaller than 30° – as expected for sets of longitudinal muscles that connect distant vertebral segments. The conspicuous medial thickening and diagonal trend of bony trabeculae in some larger osteoderms (Figs 4G and 5) could be explained as an adaptation to the loadings imposed by their participation in the carrying of the trunk.

Given the knowledge about the height of neural spines in chroniosuchians and about the distance between the main plate of the osteoderm and the transverse processes of the vertebrae (see Golubev 1998; Novikov *et al.* 2000; Clack and Klembara 2009), which possibly formed the counter-attachment for the epaxial muscles as in crocodylians, we can constrain further aspects of a chroniosuchian trunk bracing system (Fig. 12A,B): Assuming a moderate dorsal curvature of 1° per segment and a distance between osteoderm and the transverse processes which was 1.4 times as large as the axial segment length the epaxial muscles would have spanned 3–4 vertebrae. The herring-bone pattern of Sharpey's fibres in the internal cortex of the *Chroniosuchus* osteoderm FG 612/2 (Fig. 7A) probably documents an ontogenetic change in the position of neighbouring muscle insertion fields. The lack of anteroventrally dipping fibre bundles in the somewhat more laterally positioned section through three *Madygenerpeton* osteoderms (FG 596/V/13) might reflect a specific mediolateral differentiation in the attachment system (Figs 7E and 12C).

Apart from the general lack of knowledge about chroniosuchian soft body anatomy, the hypothesis of functional analogy between chroniosuchian and crocodylian osteoderm systems faces several limitations: Unlike the state of muscle attachment inferred here for chroniosuchian osteoderms, the epaxial musculature of recent eusuchians features suspension angles of <10° and only for the hyposaurine dyrosaurids, a fossil group of crocodylians with particular long neural spines, steeper angles of 20° have been suggested (Schwarz-Wings *et al.* 2009). A further dissimilarity occurs in the observed patterns of Sharpey's fibres: Despite the longitudinal trend of epaxial muscles, Sharpey's fibres in the internal cortex of *Alligator mississippiensis* (Vickaryous and Hall 2008; Klein *et al.* 2009) and fossil crocodylian osteoderms (Scheyer and Sander 2004) have transversal orientations perpendicular to the parasagittal dorsal osteoderm ridges but parallel to the orientation of cingular ligaments which are underlying the paravertebral osteoderms and form the actual attachment sites instead of a direct insertion of the muscle systems on the bone (Frey 1988*b*).

In crocodylians, successive shield segments are connected through interosteoderm ligaments that are dorsally attached to the anterior end and ventrally attached to the posterior end. Some fossil crocodylian groups display a serial overlap of narrow anterodorsal and posteroventral facets which form the insertion sites of interosteoderm ligaments (Frey 1988*b*; Salisbury and Frey 2000). In contrast, chroniosuchids display broad anteroventral and posterodorsal facets with no indication of ligament attachment (Fig. 7A,E,G,I). However, at the anterior end of two osteoderms in specimen FG 696/V/13 (Fig. 7E,F) and at posterior end of the raised ornamented dorsal area in FG 696/V/13 and FG 612/2 (Fig. 7A,B), thin bundles of craniocaudally trending Sharpey's fibres occur, and we compare them to so-called peripheral Sharpey's fibres of some squamates (Levrat-Calviac and Zylberberg 1986; de Buffrénil *et al.* 2010) and the armadillo (Vickaryous and Hall 2006) which mark the insertion of ligaments connecting neighbouring osteoderms (see Fig. 12B,C). Considering the differences in the orientation of Sharpey's fibres, the distinct articulation between osteoderms, and the position of the interosteoderm ligaments with respect to the articulation facets, the crocodylian trunk bracing systems probably shared not much more than the basic principle with chroniosuchian trunk constructions and all conclusions by analogy have to be treated with caution.

Apart from osteohistological similarities, Clack and Klembara (2009) compared the morphology of chroniosuchian osteoderm systems to the 'closed' osteoderm shields of certain fossil crocodylians, such as *Goniopholis*, whose overlap of shield segments was probably efficient in the mitigation of damaging shear and torsional loads acting on the vertebral column during raised gait on land (see Salisbury and Frey 2000). Given the lack of Sharpey's fibres in the internal cortex of *Bystrowiella schumanni* (see Witzmann and Soler-Gijón 2010) and considering the multifold overlap in the osteoderm articulations of chroniosuchians, exceeding those of crocodylians in complexity, Buchwitz and Voigt (2010) argued that the stabilisation provided by osteoderm interlock and fixation to the vertebral column was the major function of chroniosuchian osteoderm shields and probably present in the ancestor of all yet known members of the Chroniosuchia. However, if the skeletal and soft body elements forming the chroniosuchian trunk bracing system evolved closely linked in the context of terrestrialisation, both functions, i.e. suspension of epaxial muscles and support by high-degree interlock of bone, could have arisen simultaneously. To assess the ancestral state in chroniosuchians phylogenetically, further histological evidence from bystrowianid osteoderms, which have not been sufficiently covered here, is required.

Lifestyle inference from the compactness analysis of osteoderm bone

Variation in the compactness and relative thickness of spongious and compact bone layers has been shown to be correlated with lifestyle: In aquatic tetrapods inhabiting shallow water, the average compactness and overall mass of the skeleton are often higher than in the skeletons of similarly sized terrestrial dwellers, effecting a relatively low buoyancy (e.g. Francillon-Vieillot *et al.* 1990; Laurin *et al.* 2004). Secondarily, aquatic tetrapods increase the amount of bone by pachyostosis, i.e. additional accretion of cortical bone, or by osteosclerosis, i.e. increase in bone compactness, or a mixture of both (see de Ricqlès and de Buffrénil 2001; Houssaye 2009). To quantify the lifestyle-dependent variation in bone compactness, several recent approaches on extant and fossil tetrapods employ the software Bone Profiler for extracting compactness parameters from medial sections of limb bones (e.g. Laurin *et al.* 2004, 2006; Germain and Laurin 2005; Kriloff *et al.* 2008; Canoville and Laurin 2009, 2010). On the basis of the digitalised bone outline and internal spaces Bone Profiler calculates a centre to surface compactness profile and deduces several compactness parameters related to an interpolated compactness curve (see Girondot and Laurin 2003). As the known aquatic or terrestrial habitat preference of recent tetrapods is well reflected by variation in the long bone compactness parameters, lifestyle inference is feasible for fossil taxa whose ecology is poorly known or ambiguous.

Apart from the long bones, the integumentary skeleton also varies in its compactness and distribution of internal space and these variations may depend on lifestyle as well. In a first quantification approach, Scheyer and Sander (2009) have carried out Bone Profiler analyses on 15 osteoderms of pareiasaurs, crocodylians, ankylosaurs, turtles and lepidosaurs. They found some accordance between the previously assumed lifestyle and overall compactness but sample size and interfering signals (e.g. osteoderm size, variability within an individual) prevented a numerical discrimination on the basis of compactness parameters. We use a somewhat different approach here (see Fig. 3) as flat dermal bone is rather badly described by a measurement scheme that integrates over concentric osteoderm zones for a single centre to surface compactness profile and thereby neglects the strict orientation dependence of dermal bone growth and marked difference of developmental processes on the outer and inner bone surfaces.

The results for 24 dorsoventral compactness profiles of ten chroniosuchian osteoderms and their comparison to temnospondyl profiles and to the data set of Scheyer and Sander (2009) lead us to question the idea that chroniosuchians had a homogenous lifestyle: For osteoderms of *Chroniosuchus* and cf. *Uralerpeton*, which feature a relatively thick trabecular middle region, the measured overall compactness varies between 52% and 74% (see Table 3, Fig. 8A–C) – covering a range that also comprises the much thicker osteoderms of the dissorophid temnospondyl *Aspidosaurus* (Figs 8J and 9), pareiasaurs and an indeterminate nodosaur (Scheyer and Sander 2009, table 2). According to this overlap with chiefly terrestrial groups, the osteoderms of *Chroniosuchus* and cf. *Uralerpeton* did probably not serve as a means to decrease buoyancy, indicating that their bearers were probably no

aquatic animals. In contrast, the one included osteoderm of *Bystrowiella* delivers high overall compactness values between 83% and 93% similar to the dorsal osteoderms of the aquatic plagiosaurids (see Fig. 8H,I) and to amphibious crocodylomorphs but also in the range of various terrestrial amniotes (from the sample of Scheyer and Sander 2009). Nonetheless, given the relatively thick cortices which are unusually well vascularised compared to other chroniosuchians – as in the case of pachyostotic thickening (see de Ricqlès and de Buffrénil 2001) – as well as the only thin cancellous layer and lack of secondary bone, which may indicate osteosclerosis by inhibition of remodelling, we consider the osteoderm bearer as an aquatic or amphibious animal.

In accordance with a total compactness of 72–85% which is intermediate between the *B. schumanni* specimen and the osteoderms of cf. *Uralerpeton* and *Chroniosuchus*, the osteoderm samples of *Chroniosaurus* and *Madygenerpeton* display cortices of intermediate thickness and resorption of primary bone in the middle region is either not as high as in the two other chroniosuchids or a thick lining of secondary bone occurs that causes a relatively high compactness of the cancellous middle region (see Figs. 3, 5A, 6A and 8D–F). The straightforward interpretation that *Chroniosaurus* and *Madygenerpeton* had a more waterbound lifestyle than *Chroniosuchus* and cf. *Uralerpeton* but not as waterbound as *Bystrowiella* is weakened by the uncertain ontogenetic status of the individuals from which the samples of *Chroniosaurus* and *Bystrowiella* have been taken and by the possibility that the thinnest osteoderms of *Chroniosaurus* could not have been as lightly built as thicker ones for mechanical reasons (as for the lepidosaur samples of Scheyer and Sander 2009; see also size/compactness relationship in Fig. 9D). The largest osteoderms of *Chroniosaurus dongusensis* reached a medial length of about 1.4 cm whereas the specimens sectioned here were below 1 cm in length. Similarly, the sectioned *Bystrowiella* specimen SMNS 91226 is more than 40% smaller than the holotype (see Witzmann *et al.* 2008). Accordingly, only for *M. pustulatus*, whose preserved pattern of LAGs suggests an adult stage, a clear implication of more aquatic lifestyle than in *Chroniosuchus* and cf. *Uralerpeton* is given. In contrast, the high compactness of the *Chroniosaurus* and *Bystrowiella* osteoderms might be the consequence of an earlier ontogenetic stage and is thus a less compelling indication for a more waterbound lifestyle.

The inference of a more aquatic lifestyle from the compactness profiles of *M. pustulatus* osteoderms is in agreement with the peculiar morphology of their osteoderm-osteoderm articulation which indicates that the osteoderm-bearer had a laterally more flexible trunk than the wide-armoured Permian chroniosuchids and was probably more capable of axial undulation swimming (Buchwitz and Voigt 2010). The unique presence of resting lines in the cortices of the *Madygenerpeton* osteoderms could be either lifestyle-related as well or the consequence of a distinct palaeoenvironment. As the Kyrgyz depositional area of the Madygen Formation was lying between 30° and 40°N during the Middle to Late Triassic (Fedorenko and Miletenko 2002) at a similar latitude as the Russian chroniosuchid localities during the Late Permian (see Ziegler *et al.* 1997, fig. 8.3, 8.4), a higher seasonality or a lower annual average temperature are arguably not the answer to why periodical growth cessations occurred in *Madygenerpeton* and not in the Russian chroniosuchids.

Considering the strong correlation of the 20%-layer compactness values L1 to L5 for our sample of 31 measurement sections (Table 4), we have not carried out a multivariate analysis (see Laurin *et al.* 2004 and subsequent approaches) to discriminate taxa or lifestyles on the basis of these data. However, the compactness ratio of the second and fifth layer (L2/L5) provides a systematic distinction between chroniosuchids and other considered taxa: Chroniosuchid osteoderms of similar total compactness mostly have a lower L2/L5 ratio than non-chroniosuchids (Fig. 9C) which is a consequence of their typical disproportionateness between internal and external cortices. Arguably, our model of the osteoderm as a platy object that consists of locally parallel layers of homogenous compactness could yield a functioning lifestyle discrimination model – if a large enough sample of osteoderm sections and a refined layering are considered.

Conclusions

Unique among stem-amniotes, the dorsal osteoderm systems of chroniosuchians evolved convergent to similar dermal ossifications in temnospondyls and amniotes but with a common inventory of microstructures and developmental processes. Given certain similarities, such as the involvement of metaplastic ossification and a marked difference in the bone accretion rates on the inside and outside of the osteoderms, their independent origin within the two principal groups of Chroniosuchia, Chroniosuchidae and Bystrowianidae, cannot be confirmed on the basis of the present histological comparison of 13 chroniosuchid osteoderms from four species and one bystrowianid osteoderm. The chroniosuchid osteoderms feature sets of antero- and posteroventrally trending Sharpey's fibres in the non-overlapping medial part of the internal cortex which indicate the insertion of epaxial muscle systems to the ventral side of the osteoderms. Considering their attachment to the spinous processes of the vertebrae, the highly sophisticated interlocking mechanism, and their allometric medial thickening that led to a higher mechanical resistance, we interpret the muscle connection of the osteoderms not as a further anchoring element but as the part of a trunk-carrying construction that parallels the crocodylian trunk-bracing systems. This finding supports the hypothesis that the chroniosuchian osteoderm series evolved in a terrestrial context and primarily served as a device that supported terrestrial locomotion. In conflict with a homogenous terrestrial habitat and lifestyle, however, the compactness of chroniosuchian osteoderms is highly variable, indicating a differentiation of the Chroniosuchia within the aquatic-terrestrial spectrum.

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References

Amalitzky, V. P. 1921. *Seymouriidae*, North Dvina Excavations of Professor V P. Amalitzky, II, pp 1–4. Petrograd Academy of Sciences. (In Russian.)

Buchwitz, M. and Voigt, S. 2010. Peculiar carapace structure of a Triassic chroniosuchian implies evolutionary shift in trunk flexibility. – *Journal of Vertebrate Paleontology* **30**: 1697–1708.

de Buffrénil, V., Sire, J. Y. and Rage, J.-C. 2010. The histological structure of glyptosaurine osteoderms (Squamata: Anguidae), and the problem of osteoderm development in squamates. – *Journal of Morphology* **271**: 729–737.

Bystrow, A. P. 1940. On the microstructure of armour elements of Kotlassia prima Amalitzky. – *Isvestiya Akademii Nauk SSSR* **1940**: 125–127. (In Russian.)

Canoville, A. and Laurin, M. 2009. Microanatomical diversity of the humerus and lifestyle in lissamphibians. – *Acta Zoologica* **90**: 110–122.

Canoville, A. and Laurin, M. 2010. Evolution of humeral microanatomy and lifestyle in amniotes, and some comments on palaeobiological inferences. – *Biological Journal of the Linnean Society* **100**: 384–406.

Carroll, R. L. and Gaskill, P. 1978. The Order Microsauria. – *Memoirs of the American Philosophical Society* **126**: 1–211.

Castanet, J., Francillon-Vieillot, H., Meunier, F. J. and de Ricqlès, A. 1993. Bone and individual aging. In: Hall, B. K. (Ed.): *Bone. Volume 7: Bone Growth – B*, pp. 245–283. CRC Press, Boca Raton.

Cerda, I. A. and Desojo, J. B. in press. Dermal armour histology of aetosaurs (Archosauria: Pseudosuchia), from the Upper Triassic of Argentina and Brazil. – *Lethaia*. doi: 10.1111/j.1502-3931.2010.00252.x.

Cerda, I. A. and Powell, J. E. 2010. Dermal armor histology of *Saltasaurus loricatus*, an Upper Cretaceous sauropod dinosaur from Northwest Argentina. – *Acta Palaeontologica Polonica* **55**: 389–398.

Clack, J. A. and Klembara, J. 2009. An articulated specimen of *Chroniosaurus dongusensis*, and the morphology and relationships of the chroniosuchids. – *Special Papers in Palaeontology* **81**: 15–42.

Dilkes, D. 2009. Comparison and biomechanical interpretations of the vertebrae and osteoderms of *Cacops aspidephorus* and *Dissorophus multicinctus* (Temnospondyli, Dissorophidae). – *Journal of Vertebrate Paleontology* **29**: 1013–1021.

Dilkes, D. and Brown, L. E. 2007. Biomechanics of the vertebrae and associated osteoderms of the Permian amphibian *Cacops aspidephorus*. – *Journal of Zoology* **271**: 396–407.

Fedorenko, O. A. and Miletenko, N. V. (Eds.) 2002. *Atlas of the Lithology-Paleogeographical, Structural, Palinspatic and Geoenvironmental Maps of Central Asia*. Scientific Research Institute of Natural Resources YUGGEO, Almaty.

Fraas, E. 1896. *Die schwäbischen Triassaurier nach dem Material der Königlichen Naturalien-Sammlung in Stuttgart zusammengestellt*. Schweizerbart, Stuttgart.

Francillon-Vieillot, H., de Buffrénil, V., Castanet, J., Géraudie, J., Meunier, F. J., Sire, J. Y., Zylberberg, L. and de Ricqlès, A. 1990. Microstructure and mineralization of vertebrate skeletal tissues. In: Carter, J. G. (Ed.): *Skeletal Biomineralization: Patterns, Process and Evolutionary Trends*, pp. 471–548. Van Nostrand Reinhold, New York.

Frey, E. 1988a. Anatomie des Körperstammes von *Alligator mississippiensis* Daudin. – *Stuttgarter Beiträge zur Naturkunde Serie A* **424**: 1–106.

Frey, E. 1988b. Das Tragsystem der Krokodile – eine biomechanische und phylogenetische Analyse. – *Stuttgarter Beiträge zur Naturkunde Serie A* **426**: 1–60.

Germain, D. and Laurin, M. 2005. Microanatomy of the radius and lifestyle in amniotes (Vertebrata, Tetrapoda). – *Zoologica Scripta* **34**: 335–350.

Girondot, M. and Laurin, M. 2003. Bone profiler: a tool to quantify, model, and statistically compare bone section compactness profiles. – *Journal of Vertebrate Paleontology* **23**: 458–461.

Golubev, V. K. 1998. Narrow-armored chroniosuchians (Amphibia, Anthracosauromorpha) from the Late Permian of Eastern Europe. – *Paleontological Journal* **32**: 278–287.

Golubev, V. K. 2000. Permian and Triassic chroniosuchians and biostratigraphy of the Upper Tatarian series in Eastern Europe. – *Trudy Paleontologicheskogo Instituta (Moscow)* **276**: 1–175. (In Russian.)

Haines, R. W. and Mohuiddin, A. 1968. Metaplastic bone. – *Journal of Anatomy* **103**: 527–538.

Hartmann-Weinberg, A. P. 1935. The dermal ossifications of the Russian seymouriamorphs. – *Trudy Paleozoologicheskogo Instituta Akademii Nauk SSSR* **4**: 53–67. (In Russian.)

Hill, R. V. 2005. Integration of morphological data sets for phylogenetic analysis of Amniota: the importance of integumentary characters and increased taxonomic sampling. – *Systematic Biology* **54**: 1–18.

Hill, R. V. 2006. Comparative anatomy and histology of xenarthran osteoderms. – *Journal of Morphology* **267**: 1441–1460.

Houssaye, A. 2009. "Pachyostosis" in aquatic amniotes: a review. – *Integrative Zoology* **4**: 325–340.

Ivakhnenko, M. F. and Tverdokhlebova, G. I. 1980. *Systematics, morphology, and stratigraphic significance of the Upper Permian chroniosuchians from the east of the European part of the USSR*, pp. 3–68. Izdatelstvo Saratovskogo Universiteta, Saratov. (In Russian.)

Klein, N., Scheyer, T. M. and Tütken, T. 2009. Skeletochronology and isotopic analysis of a captive individual of *Alligator mississippiensis* Daudin, 1802. – *Fossil Record* **12**: 121–131.

Klembara, J., Clack, J. and Čerňanský, A. 2010. The anatomy of palate of *Chroniosaurus dongusensis* (Chroniosuchia, Chroniosuchidae) from the Upper Permian of Russia. – *Palaeontology* **53**: 1147–1153.

Kriloff, A., Germain, D., Canoville, A., Vincent, P., Sache, M. and Laurin, M. 2008. Evolution of bone microanatomy of the tetrapod tibia and its use in palaeobiological inference. – *Journal of Evolutionary Biology* **21**: 807–826.

Laurin, M. and Reisz, R. R. 1997. A new perspective on tetrapod phylogeny. In: Sumida, S. S. and Martin, K. L. M. (Eds.): *Amniote Origins: Completing the Transition to Land*, pp. 9–59. Academic Press, London.

Laurin, M., Girondot, M. and Loth, M.-M. 2004. The evolution of long bone microstructure and lifestyle in lissamphibians. – *Paleobiology* **30**: 589–613.

Laurin, M., Germain, D., Steyer, J.-S. and Girondot, M. 2006. Microanatomical data and the conquest of land by vertebrates. – *Comptes Rendus Palevol* **5**: 603–618.

Levrat-Calviac, V. and Zylberberg, L. 1986. The structure of the osteoderms in the Gekko: *Tarentola mauritanica*. – *American Journal of Anatomy* **176**: 437–446.

Li, J.-L. and Cheng, Z.-W. 1999. New anthracosaur and temnospondyl amphibians from Gansu, China. – *Vertebrata PalAsiatica* **37**: 234–247.

Main, R. P., de Ricqlès, A., Horner, J. R. and Padian, K. 2005. The evolution and function of thyreophoran dinosaur scutes: implications for plate function in stegosaurs. – *Paleobiology* **31**: 291–314.

Martin, J. E. and Benton, M. J. 2008. Crown clades in vertebrate nomenclature: correcting the definition of Crocodylia. – *Systematic Biology* **57**: 173–181.

Novikov, I. V. and Shishkin, M. A. 2000. Triassic chroniosuchians (Amphibia, Anthracosauromorpha) and the evolution of the trunk dermal ossifications in the bystrowianids. – *Paleontological Journal* **34** (Suppl) 165–178.

Novikov, I. V., Shishkin, M. A. and Golubev, V. K. 2000. Permian and Triassic anthracosaurs from Eastern Europe. In: Shishkin, M., Benton, A. M. J., Unwin, D. M. and Kurochkin, E. N. (Eds.): *The Age of Dinosaurs in Russia and Mongolia*, pp. 60–70. Cambridge University Press, Cambridge.

Peabody, F. E. 1961. Annual growth zones in living and fossil vertebrates. – *Journal of Morphology* **108**: 11–62.

Riabinin, A. N. and Shishkin, M. A. 1962.On the Upper Permian labyrinthodont *Jugosuchus*. – *Paleontologicheskii Zhurnal* **1962**: 140–1045. (In Russian.)

de Ricqlès, A. and de Buffrénil, V. 2001. Bone histology, heterochronies, and the return of tetrapods to life in water: Where are we? In: Mazin, J.-M. and de Buffrénil, V. (Eds.): *Secondary Adaptations of Tetrapods to Life in Water*, pp. 289–310. Verlag Pfeil, Munich.

de Ricqlès, A., Pereda Superbiola, X., Gasparini, Z. and Olivero, E. 2001. Histology of dermal ossifications in an ankylosaurian dinosaur from the Late Cretaceous of Antarctica. – *Asociación Paleontológica Argentina, Publicación Especial* **7**: 171–174.

Ruibal, R. and Shoemaker, V. 1984. Osteoderms in anurans. – *Journal of Herpetology* **18**: 313–328.

Ruta, M., Coates, M. I. and Quicke, D. L. J. 2003. Early tetrapod relationships revisited. – *Biological Reviews* **78**: 251–345.

Salisbury, S. W. and Frey, E. 2000. A biomechanical transformation model for the evolution of semi-spheroidal articulations between adjoining vertebral bodies in crocodilians. In: Grigg, G. C., Seebacher, F. and Franklin, C. E. (Eds.): *Crocodilian Biology and Evolution*, pp. 85–134. Surrey Beatty and Sons, Chipping Norton.

Scheyer, T. M. 2007. Skeletal histology of the dermal armor of Placodontia: the occurrence of 'postcranial fibro-cartilaginous bone' and its developmental implications. – *Journal of Anatomy* **211**: 737–753.

Scheyer, T. M. and Anquetin, J. 2008. Bone histology of the Middle Jurassic turtle shell remains from Kirtlington, Oxfordshire, England. – *Lethaia* **41**: 85–96.

Scheyer, T. M. and Sánchez-Villagra, M. R. 2007. Carapace bone histology of the giant pleurodiran turtle *Stupendemys geographicus*: phylogeny and function. – *Acta Palaeontologica Polonica* **52**: 137–154.

Scheyer, T. M. and Sander, P. M. 2004. Histology of ankylosaur osteoderms: implications for systematics and function. – *Journal of Vertebrate Paleontology* **24**: 874–893.

Scheyer, T. M. and Sander, P. M. 2009. Bone microstructures and mode of skeletogenesis in osteoderms of three pareiasaur taxa from the Permian of South Africa. – *Journal of Evolutionary Biology* **22**: 1153–1162.

Scheyer, T. M., Klein, N. and Sander, P. M. 2010. Developmental palaeontology of Reptilia as revealed by histological studies. – *Seminars in Cell and Developmental Biology* **21**: 462–470.

Schoch, R. R., Voigt, S. and Buchwitz, M. 2010. A chroniosuchid from the Triassic of Kyrgyzstan and analysis of chroniosuchian relationships. – *Zoological Journal of the Linnaean Society* **160**: 515–530.

Schwarz-Wings, D., Frey, E. and Martin, T. 2009. Reconstruction of the bracing system of the trunk and tail in hyposaurine dyrosaurids (Crocodylomorpha; Mesoeucrocodylia). – *Journal of Vertebrate Paleontology* **29**: 453–472.

Sennikov, A. G. 1996. Evolution of the Permian and Triassic tetrapod communities of Eastern Europe. – *Palaeogeography, Palaeoclimatology, Palaeoecology* **120**: 331–351.

Sennikov, A. G., Gubin, Y. M., Golubev, V. K., Bulanov, V. V., Ivakhnenko, M. F. and Kurkin, A. A. 2003. A New Oryctocoenosis of the Aquatic Vertebrate Community from the Late Permian of Central Russia. – *Paleontological Journal* **37**: 417–424.

Tatarinov, L. P. 1972. Seymouriamorphen aus der Fauna der UdSSR. In: Kuhn, O. (Ed.): *Encyclopedia of Paleoherpetology. Part 5B: Batrachosauria (Anthracosauria) Gephyrostegida – Chroniosuchida*, pp. 70–80, Gustav Fischer, Stuttgart.

Tverdokhlebova, G. I. 1972. New batrachosaurian genus from the Upper Permian of the southern Cis-Urals. – *Paleontologicheskii Zhurnal*, pp 95–103. (In Russian.)

Vallin, G. and Laurin, M. 2004. Cranial morphology and affinities of *Microbrachis*, and a reappraisal of the phylogeny and lifestyle of the first amphibians. – *Journal of Vertebrate Paleontology* **24**: 56–72.

Vickaryous, M. K. and Hall, B. K. 2006. Osteoderm morphology and development in the Nine-Banded Armadillo, *Dasypus novemcinctus* (Mammalia, Xenarthra, Cingulata). – *Journal of Morphology* **267**: 1273–1283.

Vickaryous, M. K. and Hall, B. K. 2008. Development of the dermal skeleton in *Alligator mississippiensis* (Archosauria, Crocodylia) with comments on the homology of osteoderms. – *Journal of Morphology* **269**: 398–422.

V'yushkov, B. P. 1957a. New peculiar animals from strata of the Tatarian Stage in the European part of the USSR. – *Doklady Akademiya Nauk SSSR* **113**: 183–186. (In Russian.)

V'yushkov, B. P. 1957b. New kotlassiomorphs from the Tatarian series in the European part of the USSR. – *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* **68**: 89–107. (In Russian.)

Witzmann, F. 2009. Comparative histology of sculptured dermal bones in basal tetrapods, and the implications for the soft tissue dermis. – *Palaeodiversity* **2**: 233–270.

Witzmann, F. and Soler-Gijón, R. 2010. The bone histology of osteoderms in temnospondyl amphibians and in the chroniosuchian *Bystrowiella*. – *Acta Zoologica* **91**: 96–114.

Witzmann, F., Schoch, R. R. and Maisch, M. W. 2008. A relic basal tetrapod from the Middle Triassic of Germany. – *Naturwissenschaften* **95**: 67–72.

Young, C. C. 1979. A new Late Permian fauna from Jiyuan, Honan. – *Vertebrata Palasiatica* **17**: 99–113.

Ziegler, A. M., Hulver, M. L. and Rowley, B. R. 1997. Permian world topography and climate. In: Martin, I. P. (Ed.): *Late glacial and postglacial environmental changes: Quaternary, Carboniferous-Permian and Proterozoic*, pp. 111–146. Oxford University Press, New York/Oxford.

Zylberberg, L. and Castanet, J. 1985. New data on the structure and the growth of the osteoderms in the reptile *Anguis fragilis* L(Anguidae. Squamata). – *Journal of Morphology* **186**: 327–342.

Supporting Information

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Structure of dermal scales in early tetrapods and tetrapodomorph fishes

Appendix 8

Witzmann, F. 2007. The evolution of the scalation pattern in temnospondyl amphibians. – Zoological Journal of the Linnean Society 150: 815–834.

Zoological Journal of the Linnean Society, 2007, **150**, 815–834. With 8 figures

The evolution of the scalation pattern in temnospondyl amphibians

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In most Palaeozoic temnospondyls, thin round-oval scales covering the flanks and the back of the trunk can be distinguished from ventral, elongate gastral scales arranged in a chevron pattern. The extensive growth series of the temnospondyl *Sclerocephalus* reveals that the morphology of the gastral scales in small larvae corresponds to the round-oval scales of the rest of the body. During subsequent ontogeny, the gastral scales differentiate and attain a spindle-shaped morphology. The tapering end of each gastral scale fits into a dorsal groove on the medial adjacent scale. This arrangement allowed telescoping of the scales and thus provided a high degree of flexibility. In the ontogenetically most advanced specimens of *Sclerocephalus* the gastral scales attain a rhomboid outline, and the articulation by well-defined facets has reduced the flexibility between them. In most temnospondyls, the gastral scales retain the 'juvenile' spindle-shape or the 'larval' round-oval shape, which can be interpreted as a paedomorphic trait. This suggests that the different types of gastral scales in temnospondyls, as well as the scales of the back and the flanks, can be traced back to the same *Anlage* of round-oval scales that differentiated early in ontogeny. In the Mesozoic, a complete reduction of dermal scalation occurred independently in distinct dissorophoid, capitosauroid, and trematosauroid temnospondyls. This reduction was probably the result of several factors unique to each group, such as cutaneous respiration, the demand for greater mobility, and the decreased importance of belly protection in fully aquatic temnospondyls.

ADDITIONAL KEYWORDS: cutaneous respiration – dermal scales – integument – ontogeny – paedomorphosis – phylogeny.

The presence of ossified dermal scales covering the body is widespread in temnospondyls and other basal tetrapods of the Palaeozoic, and is likely to be a heritage from their fish ancestors (Dias & Richter, 2002; Castanet *et al.*, 2003). In contrast to Palaeozoic sarcopterygian fish, the earliest known tetrapods have eliminated the enamel and dental components of their scales, in convergence with most extant fish (Colbert, 1955; Dias & Richter, 2002; Castanet *et al.*, 2003).

The first in-depth study of dermal scalation in a temnospondyl (and Palaeozoic basal tetrapod) was provided by von Meyer (1858) in his monograph on *Archegosaurus decheni* Goldfuss, 1847. Von Meyer recognized two different types of dermal scales: spindle-shaped scales that form rows arranged in a chevron pattern (a repeated Λ pattern) on the ventral side of the trunk between the pectoral girdle and the pelvis, and thin cycloid or oval scales that cover the flanks and the dorsal portion of the trunk as well as the limbs. Further descriptions of basal tetrapod scales were given by Fritsch (1883, 1889) in his work on the fauna of the gas coal in Nýřany and Credner (1881, 1886, 1893) involving the scalation of 'branchiosaurs' of the Döhlen Basin in Saxony. Dermal scales have been subsequently reported in a variety of different temnospondyl taxa. Broili (1926, 1927), Boy (1988), and recently Schoch (2003) commented on the scalation in the actinodontid *Sclerocephalus*, and scale morphology and their arrangement in different dissorophoids were described by Steen (1931), Gregory (1950), Boy (1972, 1978, 1986, 1987), Werneburg (1987, 1994), and Daly (1994). Case (1935) described dermal scales in *Trimerorhachis*, as did Romer &

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Witter (1941) in *Eryops*. In 1955 Colbert published a study on scale morphology of *Trimerorhachis*, including a comparison with other temnospondyls as well as with fish and gymnophionans. His description of the scalation in *Trimerorhachis* was basically confirmed by Chase (1965) and Berman (1973) in their works on the trimerorhachids *Neldasaurus* and *Lafonius*, respectively. Studies dealing exclusively with the ventral scalation of stereospondylomorph temnospondyls were published by Findlay (1968) on *Uranocentrodon* and by Dias & Richter (2002) on *Australerpeton*. Further descriptions of dermal scales in stereospondylomorphs are included in the works of Van Hoepen (1915), Broili & Schröder (1937), Nilsson (1946), Konzhukova (1955), Watson (1958), Warren & Hutchinson (1987), Janvier (1992), Hellrung (2003), and Pawley & Warren (2004, 2005). Carroll (1967) and Milner & Sequeira (1994) demonstrated dermal scalation in the basal temnospondyls *Dendrerpeton* and *Balanerpeton*, respectively. Among extant amphibians, the occurrence of dermal scales is restricted to representatives of gymnophionans. Although Colbert (1955) regarded the scales in gymnophionans as heritage from their Palaeozoic ancestors, Zylberberg & Wake (1990) emphasized that it is equally parsimonious to assume that the gymnophionan scales are *de novo* acquisitions.

The purpose of the present paper is to analyse the evolution of scalation in temnospondyls. First, the morphology of the scales and their arrangement are described and compared in the different temnospondyl lineages. A further focus will be the documentation of the ontogeny of the scalation. Then, the plesiomorphic condition of the scalation pattern in temnospondyls will be ascertained, whereby the stem-tetrapods *Ichthyostega*, *Tulerpeton*, and *Greererpeton* are taken as the primary source for polarity determination. Finally, the functional significance of the ventral and dorsal scales in temnospondyls will be assessed in the light of the new morphological and ontogenetic data.

DEFINITION OF ANATOMICAL TERMS

Ruibal & Shoemaker (1984) used the term 'dermal scale' for the dermal ossifications of osteichthyans and gymnophionans, whereas they referred to the ossified structures in the dermis of anurans and squamates as 'osteoderms'. Zylberberg & Wake (1990) adopted this terminology and listed differences between scales and osteoderms relative to their association with soft parts (e.g. scales are located in pockets in contrast to osteoderms). They emphasized, however, that this distinction does not imply common ancestry of either dermal scales or osteoderms. Because soft parts of the dermis are mostly not preserved in basal tetrapods, the structural distinction between dermal scales and osteoderms of Castanet *et al.* (2003) is followed in the present study: osteoderms are plates of dermal bone that often bear a pitted outer surface; dermal scales, in contrast, are thinner than osteoderms, often round or elongate oval in outline, and may overlap. The present paper deals with ossifications of temnospondyls that can be interpreted as dermal scales.

The term 'gastralia' is often used to refer to the elongate ventral ossifications of basal tetrapods because their Λ-shaped arrangement closely resembles the gastralia or 'abdominal ribs' of several amniotes. Indeed, the gastralia of amniotes are probably derived from the ventral scales of basal tetrapods (Baur, 1889; Voeltzkow & Döderlein, 1901; Romer, 1956). In extant crocodilians and *Sphenodon*, the gastralia develop in the dermis and become secondarily embedded in the rectus abdominis muscle later in ontogeny (Voeltzkow & Döderlein, 1901; Howes & Swinnerton, 1901; Claessens, 2004). In contrast, the ventral scales of the temnospondyl *Australerpeton* were located in the dermis both in juveniles and adults, as Dias & Richter (2002) were able to demonstrate, and this must also be assumed for other basal tetrapods. To avoid confusion between the more rod-like gastralia of amniotes, and their probable precursors in basal tetrapods, the term 'gastralia' is avoided in the present study, and the term 'gastral scales' is used here to refer to the ventral ossifications in basal tetrapods. Similarly orientated gastral scales overlapping each other along their long axis are referred to as 'rows' (Fig. 1). Two associated rows from the same metameric segment articulating in the ventral midline are called a 'chevron'. Two posterolaterally aligned rows from opposite sides of the trunk form an anteriorly directed chevron, and two anterolaterally directed rows form a posteriorly directed chevron. The remaining round-oval scales that cover the flanks and back of the trunk, the limbs, and the tail are referred to as 'dorsal scales'.

INSTITUTIONAL ABBREVIATIONS

CMNH, Cleveland Museum of Natural History, Cleveland, OH, USA; IGS, Institut de Géologie Strasbourg, Université Louis Pasteur, Strasbourg, France; MB, Museum für Naturkunde, Humboldt Universität, Berlin, Germany; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; MMG, Staatliches Museum für Mineralogie und Geologie, Dresden, Germany; PIN, Palaeontological Institute of the Russian Academy of Sciences, Moscow, Russia; ROM, Royal Ontario Museum, Toronto, ON, Canada; SMNK, Staatliches Museum für Naturkunde, Karlsruhe, Germany; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany.

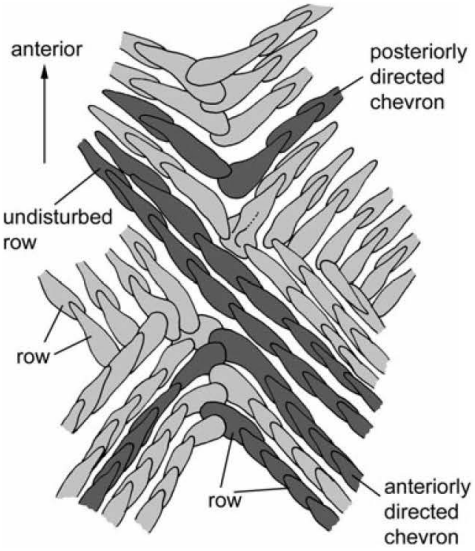

Figure 1. Schematic drawing of gastral scales in the anterior region of the belly in a temnospondyl illustrating the terms 'row', 'anteriorly directed chevron', and 'posteriorly directed chevron'.

MATERIAL EXAMINED

The skull length (sl) is used as a measure of size, herein defined as the distance from the tip of the snout to the posterior margin of the postparietals.

Archegosaurus decheni Goldfuss, 1847 from the Lower Rotliegend (Autunian) of Lebach, Saar-Nahe Basin (Saarland, south-western Germany): MB.Am.227 (sl 84 mm, complete skeleton), MB.Am.229 (sl 79 mm, complete skeleton), MB.Am.252 (sl *c.* 65 mm, almost complete skeleton including tail), MB.Am.273 (sl estimated 200 mm, pelvic region plus tail), MB.Am.289 (sl *c.* 110 mm, with anterior half of the trunk); IGS U II 3/1 (postcranial remains of large specimen).

Branchierpeton amblystomus (Credner, 1881) from the Lower Rotliegend (Autunian) of Niederhäslich, Döhlen Basin, Saxony, Germany: MMG SaP 154 (sl 15 mm, complete skeleton), MMG SaP 700 (sl 17 mm, complete skeleton).

Cheliderpeton latirostre (Jordan, 1849) from the Lower Rotliegend (Autunian) of the Saar-Nahe Basin (Saarland and Rheinland-Pfalz, south-western Germany): MB.Am.1271 (sl 58 mm, complete skeleton), MB.Am.1275 (sl 39 mm, complete skeleton), MB.Am.1293 (sl 54 mm, skull and anterior part of the trunk), MB.Am.1312 (sl 61 mm, skull and anterior part of the trunk); ROM 5735 (sl 58 mm, skull with anterior half of the trunk).

Dendrerpeton sp. from the Westphalian D of Florence, Nova Scotia: MCZ 8779 (disarticulated skull, pectoral girdle, gastral and dorsal scales).

Eryops megacephalus Cope, 1877 from the Belle Plains Formation, Wichita Group, Lower Permian, Texas, USA: MCZ 1539 (caudal vertebrae with dorsal scales), MCZ 1738 (part and counterpart of gastral scales).

Greererpeton burkemorani Romer, 1969 from Deckers Creek, West Virginia, Upper Mississippian, USA: CMNH 11073 (sl 150 mm, with anterior part of the trunk), CMNH 11219 (complete skeleton), CMNH 11233 (sl 120 mm, with complete postcranial skeleton), CMNH 11236 (trunk plus pelvic region).

Plagiosuchus pustuliferus (Fraas, 1896) from the Middle Triassic (Ladinian) of Baden Württemberg, Germany: SMNS 84794 (complete skeleton).

Platyoposaurus stuckenbergi (Trautschold, 1884) from the Upper Permian (Kazanian) of Belebey, Bashkortostan (Southern Ural), Russia: PIN 164/1–9 (interclavicle, scapulocoracoid, articulated and isolated gastral scales).

Sclerocephalus haeuseri Goldfuss, 1847 from the Lower Rotliegend (Autunian) of the Saar-Nahe Basin, Rheinland-Pfalz, south-western Germany: MB.Am.1233 (sl *c.* 80 mm, with anterior trunk), MB.Am.1298 (sl 72 mm, complete skeleton), MB.Am.1314 (sl 22 mm, complete skeleton), SMNK uncatalogued (sl 183 mm, complete skeleton); SMNS 90507 (sl 205 mm, almost complete skeleton, plaster cast of the neotype housed in the Palaeontological Institute of the University of Mainz, Germany; Boy, 1988), SMNS 90055 (sl 198 mm, complete skeleton), SMNS 54065 (sl 156 mm, complete skeleton).

Trimerorhachis insignis Cope, 1878 from the Lower Permian, Clyde Formation, Clear Fork Group, Baylor County, Texas, USA: MCZ 1080 (pectoral girdle, vertebrae, dorsal and gastral scales).

DESCRIPTION

THE ARRANGEMENT OF GASTRAL SCALES

In the vast majority of temnospondyls the gastral scales are arranged in a chevron pattern, i.e. a repeated Λ pattern. Anteriorly directed chevrons are present in the middle and posterior trunk region, whereas the chevrons are directed posteriorly in the anterior trunk region immediately posterior to the pectoral girdle (Fig. 2). A region termed the 'nodal point' by von Meyer (1858) lies between the anteriorly and posteriorly directed chevrons.

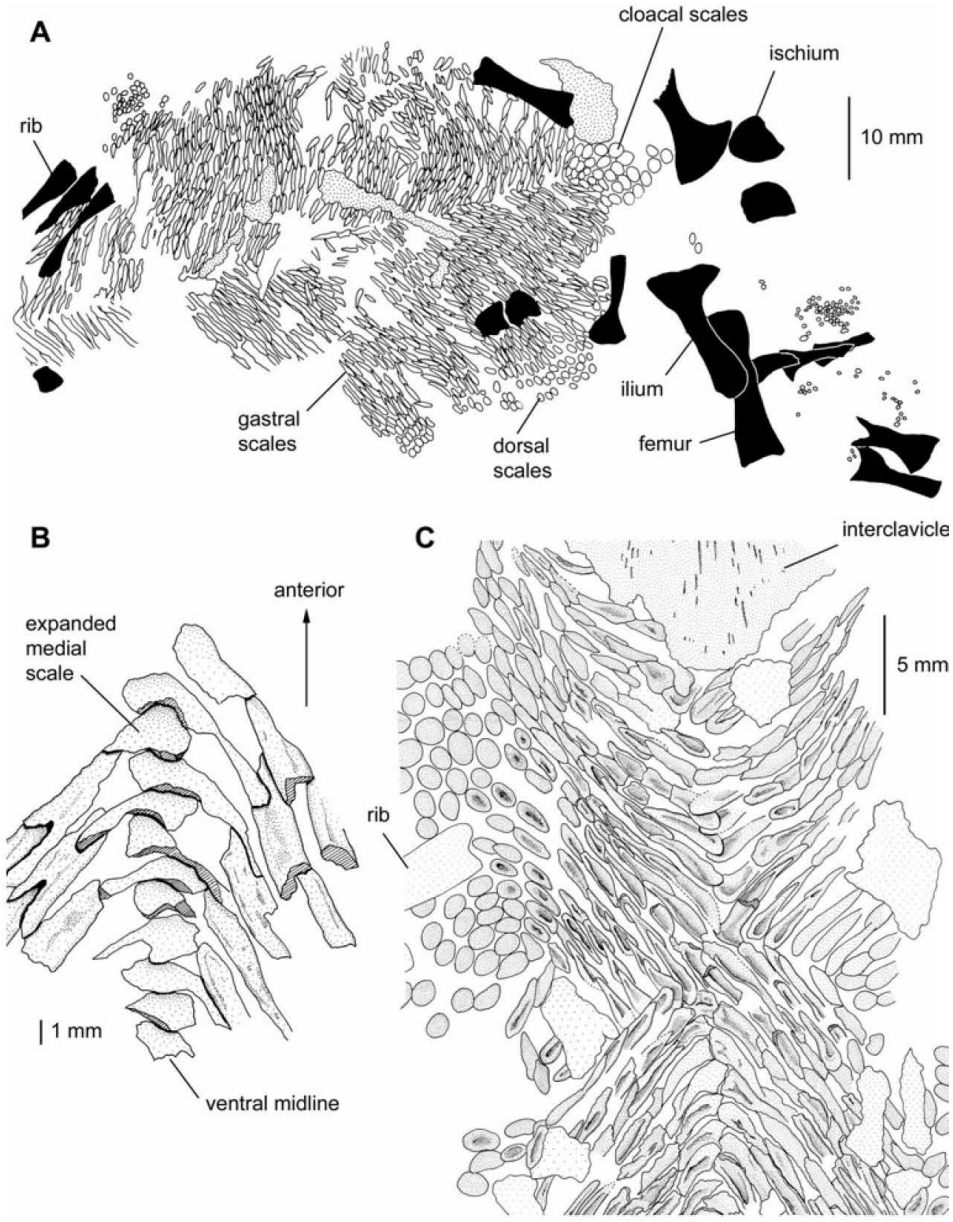

Figure 2. *Archegosaurus decheni*. A, MB.Am.229. Anteriorly directed chevrons with round-oval scales of the flanks, the cloacal region, and the hindlimb. The angle of the chevrons in the ventral midline was enlarged after the death of the animal by a slight displacement of the rows. B, MB.Am.289. Gastral scales articulating in the ventral midline of the trunk, ventral view. C, MB.Am.289. Nodal point of gastral scales in dorsal view between anteriorly and posteriorly directed chevrons.

Anteriorly directed chevrons

In most temnospondyls approximately 70–90 anteriorly directed chevrons are present, and this number does not change during ontogeny in taxa with preserved growth series, e.g. *A. decheni* and *S. haeuseri*. The posterolaterally running rows of gastral scales follow the shape of a shallow 'S' (Fig. 2A). In the first anteriorly directed chevrons the rows of gastral scales articulate in the ventral midline of the trunk, at approximately a right angle. This angle decreases gradually to approximately 60° in the posterior-most chevrons. The last chevron is located a distance of approximately two vertebrae anterior to the ilium in the temnospondyls examined. In the ventral midline of the trunk, the rows articulate in the following way (Fig. 2B): each medial-most gastral scale has a rounded medial end, the posterior portion of which is overlapped by the medial-most scale from the opposite row. The rounded medial end is expanded in some temnospondyl taxa. The overlap in the ventral midline of the trunk takes place alternating from the left and right side of the trunk, and each medial-most gastral scale articulates with two medial-most ones from opposite rows. Thus the medial-most gastral scales imbricate in the anteroposterior direction in the midline of the trunk in ventral view (Fig. 2B).

The 'nodal point'

The 'nodal point' is the point of inversion from the anteriorly to the posteriorly directed chevrons, located a short distance posterior to the end of the interclavicle. This region is rarely preserved in temnospondyls, but its rather complicated arrangement is clearly visible in specimens of *Archegosaurus*, *Sclerocephalus*, and *Branchierpeton* (Figs 1, 2C). Undisturbed rows of spindle-shaped scales run diagonally between the opposing sets of chevrons. The number of undisturbed rows in individual specimens varies from one to eight in the *Archegosaurus* and *Sclerocephalus* specimens studied. At the nodal point, a number of rows are present that run parallel to the anteriorly and posteriorly directed chevrons, respectively, but do not meet in the ventral midline. Instead, they contact the opposing rows at an angle of approximately 90° (Figs 1, 2C).

Posteriorly directed chevrons

The gastral scales of the posteriorly directed chevrons run parallel to the posterolateral margins of the interclavicle (Fig. 2C). The anterolaterally directed rows meet in the ventral midline in the same manner as described above for the anteriorly directed chevrons, so that the medial-most scales imbricate from posterior to anterior in ventral view. In most specimens of *Archegosaurus*, *Sclerocephalus*, and *Branchierpeton*, the number of posteriorly directed chevrons varies individually between eight and 12. In some individuals they may be absent altogether. Fritsch (1889: pl. 56, fig. 2) illustrated the ventral scalation of an individual of *Cheliderpeton vranyi* Fritsch, 1877 in which the first anteriorly directed chevron contacts the interclavicle, so that no undisturbed rows and no posteriorly directed chevrons are present. Instead, anterolaterally directed rows contact the anteriorly directed chevrons at an angle of about 90°. Another specimen of this species possesses posteriorly directed chevrons (Werneburg & Steyer, 2002: fig. 4a). The same pattern, as illustrated by Fritsch (1889), is visible in the rhinesuchid postcranium described by Pawley & Warren (2004: fig. 3), in *Platyoposaurus* (PIN 164/1), in *C. latirostre* (ROM 5735), and in the *Sclerocephalus* specimen MB.Am.1203, although in the latter two specimens three undisturbed rows of gastral scales are present.

MORPHOLOGY OF THE GASTRAL SCALES

The morphology of the gastral scales differs by taxon and ontogenetic stage. The gastral scales can be divided into three morphological groups with transitions between each: ovoid, spindle-shaped, and rhombic gastral scales.

Ovoid gastral scales

Ovoid gastral scales are present in the basal temnospondyl *Balanerpeton*, and among the dissorophoids in micromelerpetontids, branchiosaurids, and amphibamids, and in a derived condition in trimerorhachids. These gastral scales are broadly oval with bluntly rounded medial and lateral ends. Each scale bears concentric growth rings and is ventrally (externally) convex and dorsally (internally) concave. Within the same row of gastral scales, the medial end of each scale overlaps the dorsal surface of its medial neighbour. The degree of overlap is extensive (up to more than 50% of the scale length). The posterior margin of each gastral scale slightly overlaps the ventral surface of the neighbouring scale of the posteriorly located row.

The most plesiomorphic micromelerpetontid, *Limnogyrinus*, has thick gastral scales that are composed of two layers and bear concentric rings and radial striae (Werneburg, 1994). In contrast, the scales of the micromelerpetontids *Branchierpeton* and *Micromelerpeton* are thinner and have attained a derived morphology with anastomosing longitudinal striae on the ventral surface and tubercles on the posterior margin (Boy, 1972; Werneburg, 1991). The chevron arrangement of scales with a nodal point as described above is

especially conspicuous in *Branchierpeton* specimens (Credner, 1886: pl. 19, figs 3, 8 and 9; Werneburg, 1991: figs 11 and 15; F. Witzmann, pers. observ.: MMG SaP 154, MMG SaP 700) (Fig. 3A). Among branchiosaurids, the plesiomorphic *Branchiosaurus* has gastral scales that are similar to *Limnogyrinus* (Werneburg, 1987), whereas in other branchiosaurids the scales have become much thinner (Boy, 1993). Branchiosaurid scales are composed of a basal layer with concentric rings and a thinner upper layer with longitudinal striae (Boy, 1972). Within amphibamids, *Amphibamus* has ovoid gastral scales arranged in a chevron pattern (Gregory, 1950). Large specimens of *Platyrhinops* have poorly ossified gastral scales (Clack & Milner, 1993). The gastral scales are possibly arranged in transverse rows and not in the chevron pattern in the amphibamid *Eoscopus* (Daly, 1994).

Small larvae of the basal stereospondylomorph *S. haeuseri* also have ovoid gastral scales, e.g. MB.Am.1302 (sl 18 mm) (Fig. 3B). In the rhytidosteoid stereospondyl *Mahavisaurus*, broadly oval gastral scales are present on the ventral trunk immediately posterior to the pectoral girdle (Lehman, 1966; Janvier, 1992). The capitosauroids *Paracyclotosaurus* and *Wellesaurus* may also have ovoid gastral scales, although the situation is not unequivocal because of inadequate preservation. *Paracyclotosaurus* has irregularly set oval scales at least on the posterior part of the belly (Watson, 1958), whereas spindle-shaped gastral scales are not preserved (see below). Also in *Wellesaurus*, no spindle-shaped scales are present, but round-oval scales are visible on the trunk between the ribs (R. R. Schoch, pers. comm.) and might have covered the belly.

Trimerorhachids also possess ovoid gastral scales, but they differ from those of the other species in being anteroposteriorly elongate. In MCZ 1080, the anteriormost gastral scales are visible posterior to the interclavicle (Fig. 3C). They appear to be arranged in posteriorly directed chevrons, but this cannot be stated with certainty because of poor preservation. As in micromelerpetontids and branchiosaurids, the gastral scales of trimerorhachids consist of two layers, a thin upper layer with longitudinal striae, and a thicker lower layer with concentric rings (Colbert, 1955; Chase, 1965).

Spindle-shaped gastral scales

The majority of temnospondyls have slender, spindle-shaped gastral scales. In this morphology, one end of the scale is bluntly rounded, whereas the other end

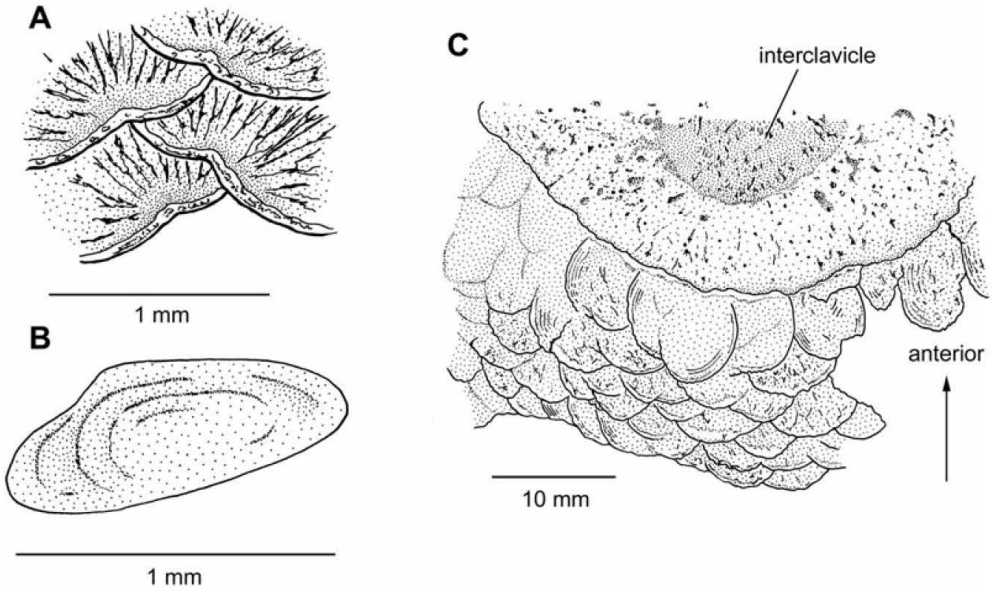

Figure 3. Ovoid gastral scales. A, *Branchierpeton amblystomus*. Gastral scales articulating in the ventral midline, redrawn after Werneburg (1991). B, *Sclerocephalus haeuseri*, MB.Am.1302. Gastral scale. C, *Trimerorhachis insignis*, MCZ 1080. Posterior part of interclavicle with gastral scales in ventral view.

tapers to a long point. Their outline is rather conservative in the different groups of temnospondyls. The following description is based on *A. decheni*, the spindle-shaped gastral scales of which possess a generalized morphology. The ventral side of each gastral scale bears a pronounced posterior ridge separated by a slight concavity from a less pronounced anterior ridge (Fig. 4A). Both ridges become more flattened towards the tapering end. In dorsal view, each gastral scale bears a deep groove and is asymmetric anteroposteriorly: the posterior margin of the dorsal groove is formed by a steep, thickened, bulge-like crest, whereas a sharp, anterodorsally directed crest delimits the groove anteriorly (Fig. 4B). The groove shallows gradually towards the tapering (medial) end, but terminates rather abruptly towards the rounded (lateral) end of the gastral scale. In the anteriorly directed chevrons, the tapering end is directed anteromedially towards the ventral midline of the trunk, and fits into the dorsal concavity of the medial neighbour (Figs 2C, 4B), whereby the degree of dorsal overlap generally amounts to more than 50% of scale length. Therefore, the gastral scales of the same row imbricate in a posterolateral direction in ventral view. In contrast, the tapering ends of the gastral scales of the posteriorly directed chevrons point anterolaterally (in the direction to the flanks) (Fig. 2C); thus the gastral scales of each row imbricate in posteromedial direction in ventral view. The anterior-most rows consist of less elongate, mostly nonoverlapping scales that are situated on the smooth posteroventral surface of the interclavicle. Both the concave dorsal surface and the ventral side of the scales are smooth, with the exception of the aforementioned ventral ridges and short striae that are aligned with the long axis of the scale. The lateralmost gastral scale of each row is thinner than the more medially situated ones. Similar to the ovoid gastral scales and the dorsal scales (see below), these scales bear concentric growth rings. In contrast to the scalation pattern in micromelerpetontids and branchiosaurids the chevrons do not overlap each other, but the anterior margin of each gastral scale abuts against the thickened posterior margin of the adjacent gastral scale of the anterior chevron.

Boy (1988: 127, fig. 11) depicted the complete ventral trunk region of *S. haeuseri* covered with gastral scales, and considered their morphology to be highly variable and of irregular outline. However, the outline and arrangement of these scales are in fact quite regular, being virtually identical to those of *Archegosaurus* in late larval to subadult specimens of *Sclerocephalus* (skull length *c.* 20–150 mm). Spindle-shaped gastral scales of basically the same morphology are present in the basal temnospondyl *Dendrerpeton* (MCZ 8779) (Fig. 4C), in the eryopids *Eryops* (MCZ 1738) (Fig. 4D) and *Onchiodon* (Credner, 1893), in the basal stereospondylomorphs *C. vranyi* (Werneburg & Steyer, 2002) and *C. latirostre* (MB.Am.1271, MB.Am.1275, MB.Am.1293, MB.Am.1312, ROM 5735), and the stereospondyls *Uranocentrodon* (Findlay, 1968), *Lydekkerina* (Broili & Schröder, 1937; Pawley & Warren, 2005), and *Edingerella* (Lehman, 1966; Janvier, 1992: pl. 2, figs 2a, b). In the rhytidosteoid *Acerastea*, the gastral scales are proportionally more elongate than in the aforementioned taxa (Warren & Hutchinson, 1987). Plagiosaurids have proportionally the most elongate and slender gastral scales (Fig. 4E). In *Gerrothorax*, they are located on the dorsal side of plate-like ventral osteoderms. The rows are reduced in number and well separated from each other, and no articulation in the ventral midline of the trunk takes place (Nilsson, 1946; Hellrung, 2003). The gastral scales of *Plagiosuchus* are likewise very long and slender (Fig. 4E). However, the osteoderms were reduced to tiny globules that lay within the dermis (SMNS 84794). The enigmatic temnospondyl *Peltobatrachus* has small, needle-shaped gastral scales, whereas the back of the trunk and the tail are covered by plate-like osteoderms (Panchen, 1959).

Rhombic gastral scales

The stereospondylomorph *P. stuckenbergi* has well-ossified gastral scales of rhombic outline (PIN 164/1–9) (Fig. 5 A, B). In contrast to the spindle-shaped gastral scales, the anterior margins of the rhombic scales of one row overlap the posterior parts of the gastral scales of the preceding row dorsally, so that the chevrons overlap from anterior to posterior in ventral view. The gastral scales in the anterior half of the trunk are heavily ossified and thick, whereas they become thinner in the posterior half of the trunk. In ventral view, each gastral scale has a pronounced sculpture of ridges and tubercles, and several foramina penetrate the bone (Fig. 5A). Each scale possesses a ventromedial facet that overlaps the dorsal surface of the neighbouring medial gastral scale of the same row, so that the scales imbricate in posterolateral direction within each row in ventral view. In its medial portion, this ventromedial facet is convex and bears a prominent, sharp crest, whereas the lateral end of the facet is deeply concave. The dorsal (internal) side of each rhombic gastral scale bears a well-defined dorsolateral facet that constitutes approximately 60–70% of the length of the scale (Fig. 5A, right). The anterior border of this facet is formed by a deep and sharp anterodorsally directed crest, whereas the posterior border of the facet is formed by a less deep, but thick bulge. The lateral portion of this facet is convex; it becomes increasingly concave medially and forms a distinct depression. This pattern is more pronounced in the

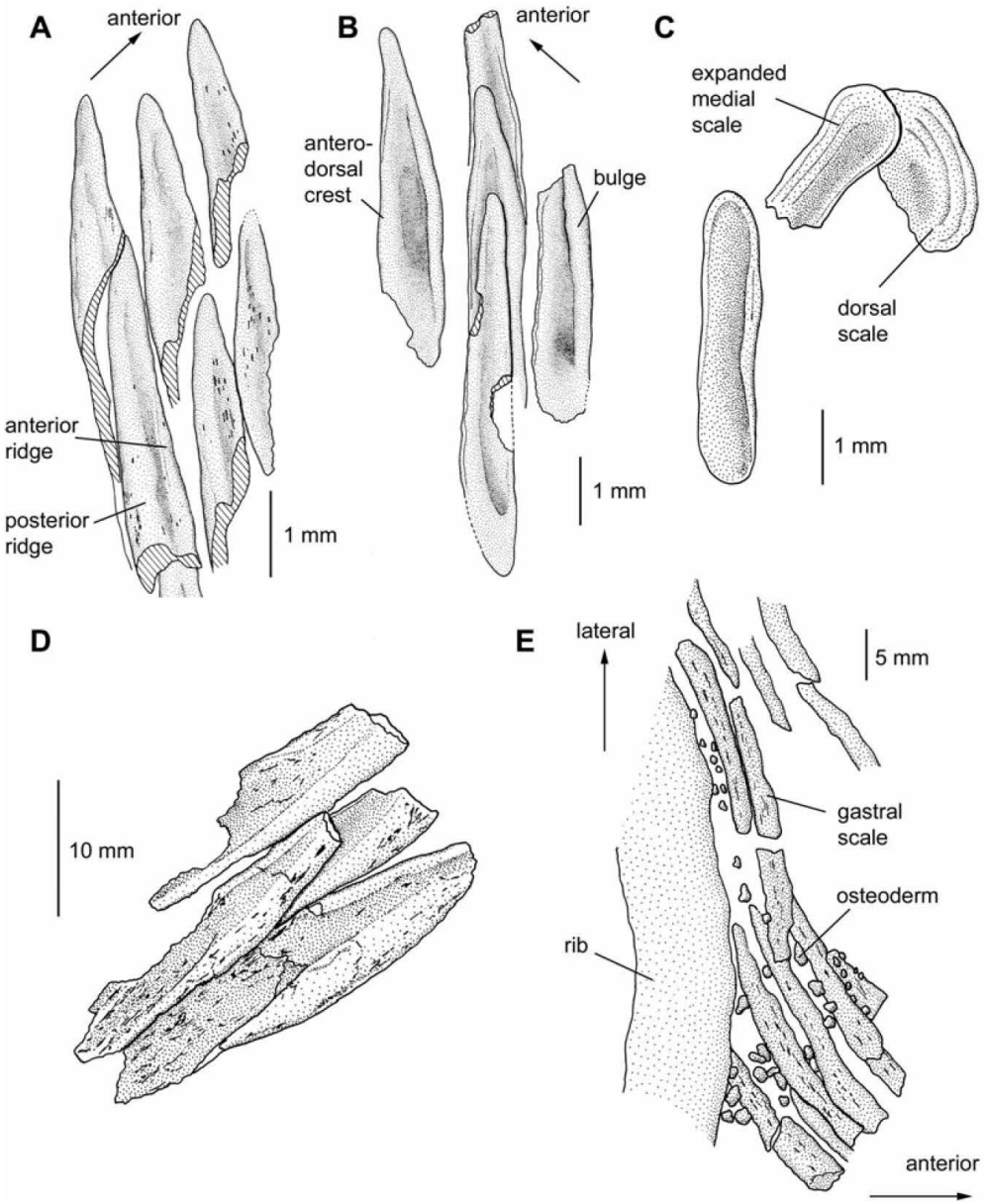

Figure 4. Spindle-shaped gastral scales. A, B, *Archegosaurus decheni*, MB.Am.289. A, gastral scales in ventral view. B, gastral scales in dorsal view. C, *Dendrerpeton* sp., MCZ 8779. Two gastral scales in dorsal view plus isolated dorsal scale. D, *Eryops megacephalus*, MCZ 1738. Gastral scales in dorsal view. E, *Plagiosuchus pustuliferus*, SMNS 84794. Gastral scales with small, globular osteoderms in dorsal view.

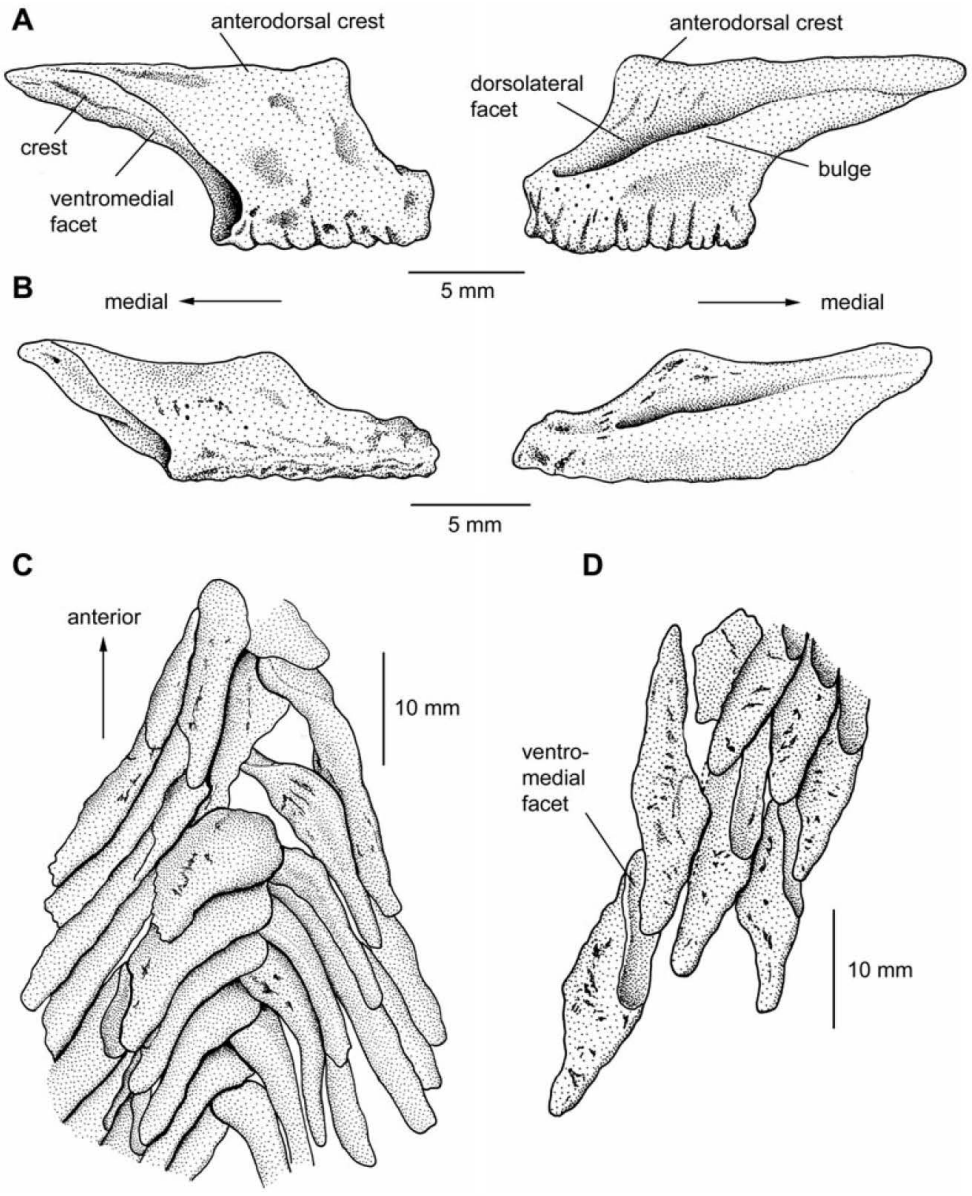

Figure 5. Rhombic gastral scales. A, B, *Platyoposaurus stuckenbergi*, PIN 164/1–9. A, isolated gastral scale, probably from the anterior part of the trunk, in anteroventral (left) and anterodorsal view (right). B, isolated gastral scale, probably from the posterior part of the trunk, in anteroventral (left) and anterodorsal view (right). C, D, *Sclerocephalus haeuseri*, SMNS 90507. C, gastral scales articulating in the ventral midline, ventral view. D, articulating gastral scales in ventral view.

more strongly ossified gastral scales of the anterior trunk region. Medial to the facet, the dorsal surface of the scale is flat and becomes slightly convex at the medial end.

The same morphology and arrangement of gastral scales as in *Platyoposaurus* is present in the largest known specimens of *S. haeuseri* (SMNS 90507, SMNS 90055; SMNK uncatalogued) (Fig. 5C, D) and the stereospondyl *Australerpeton cosgriffi* Barberena, 1998 (Dias & Richter, 2002). The postcranial skeleton of a rhinesuchid also bears rhombic gastral scales (Pawley & Warren, 2004: fig. 3).

MORPHOLOGY AND ARRANGEMENT OF THE DORSAL SCALES

In contrast to the well-ossified gastral scales, a comparison of the dorsal scales in temnospondyls is hampered by the fact that these more delicate ossifications are often not preserved or only poorly preserved, or were destroyed during preparation. As a morphological basis, the dorsal scalation of the basal stereospondylomorphs *Archegosaurus* and *Sclerocephalus* will be described first. The morphology and arrangement of the scales in these taxa is well preserved in almost all parts of the body. Subsequently, the dorsal scales of other temnospondyls are addressed.

Archegosaurus decheni

As already reported by von Meyer (1858), Jaekel (1896), and Broili (1927), the round-oval dorsal scales next to the gastral scales possess concentric growth rings and are cup-shaped, i.e. internally concave and externally convex. In contrast, the dorsal scales of the flanks and the back of the trunk are distinctly thinner and are preserved two-dimensionally. This indicates a decrease in ossification from the gastral scales of the belly to the cup-shaped scales of the ventral part of the flanks, and then to the thin scales of the flanks and the back. The dorsal scales of the trunk do not mutually overlap (Fig. 2A, C); at best, there is point contact such that there is always a space between them. This pattern does not change during ontogeny. Scales covering the limbs are smaller than those of the trunk and have a cup-like morphology with a distinct medial elevation in large specimens (e.g. IGS U II 3/1). The scales are tightly arranged but do not overlap each other. In MB.Am.229, enlarged round-oval scales are located on the ventral side immediately behind the posterior-most chevron and anterior to the base of the ilium (Fig. 2A). The long axis of such a 'cloacal scale' is approximately two times longer than that of a dorsal scale of the lateral trunk region, and four times longer than a limb scale. As illustrated by von Meyer (1858: pl. 18, figs 1, 2), similar enlarged scales are also located in the region anterior to the clavicles and the cleithra. Dorsal scales that are anteroposteriorly elongate are preserved in the lateral region of the ilium in MB.Am.273 (Fig. 6 A). They are aligned in transverse rows in such a way that each scale of one row is located between two scales of the preceding row. The dorsal scales in the tail are cup-shaped, tightly set, and possibly overlap each other slightly (MB.Am.252, MB.Am.273) (Fig. 6B), and so are more closely spaced than those of the lateral and dorsal parts of the trunk and the sacral region.

A pattern of fine undulating radial striae is visible on the scales of the tail in MB.Am.273 and is superimposed on the above-described, more pronounced concentric rings (Fig. 6B). Some very thin parts of scales found in MB.Am.273 display only the radial striations, but no concentric rings are visible. This shows that the dorsal scales of *Archegosaurus* are composed of a lower layer with concentric rings, and an upper, thinner layer that bears the radial striae.

Sclerocephalus haeuseri

The dorsal scales of *Sclerocephalus* possess the same morphology as described for *Archegosaurus*, with fine radial striae that are superimposed on the concentric rings (Schoch, 2003). As in *Archegosaurus* the dorsal scales are cup-shaped lateral to the gastral scales, and they are thin and two-dimensionally preserved on the flanks and on the back (Boy, 1988). However, in larval and juvenile *Sclerocephalus* specimens (at least until a skull length of 72 mm; MB.Am.1298), the dorsal scales overlap regularly in the manner of a shingled roof (Fig. 6C). This overlap takes place from anterior to posterior on the trunk and the tail, and from proximal to distal on the limbs. Each scale of one transverse row is positioned between two scales of the anterior transverse row. The arrangement of these scales is reconstructed schematically in Fig. 6 (D, left) as compared with the arrangement in *Archegosaurus* (Fig. 6D, right). In MB.Am.1298, dorsal scales that are smaller than those of the back and the tail are preserved on the stem and the head of the cleithrum. These scales are loosely set and have no point contact. In larger specimens of *Sclerocephalus*, the dorsal scales are mostly not perserved or only poorly preserved, so that it is difficult to determine their arrangement. In SMNK uncatalogued (sl 183 mm), dorsal scales with concentric growth rings are preserved in several regions of the trunk and the tail. The scales on the surface of the cleithrum and the scapulocoracoid are loosely set without point contact. This applies also for the scales that are preserved on the broad ribs in the anterior trunk region. In the posterior half of the trunk, the scales are more tightly set but do not overlap. At least on the flanks, the scales

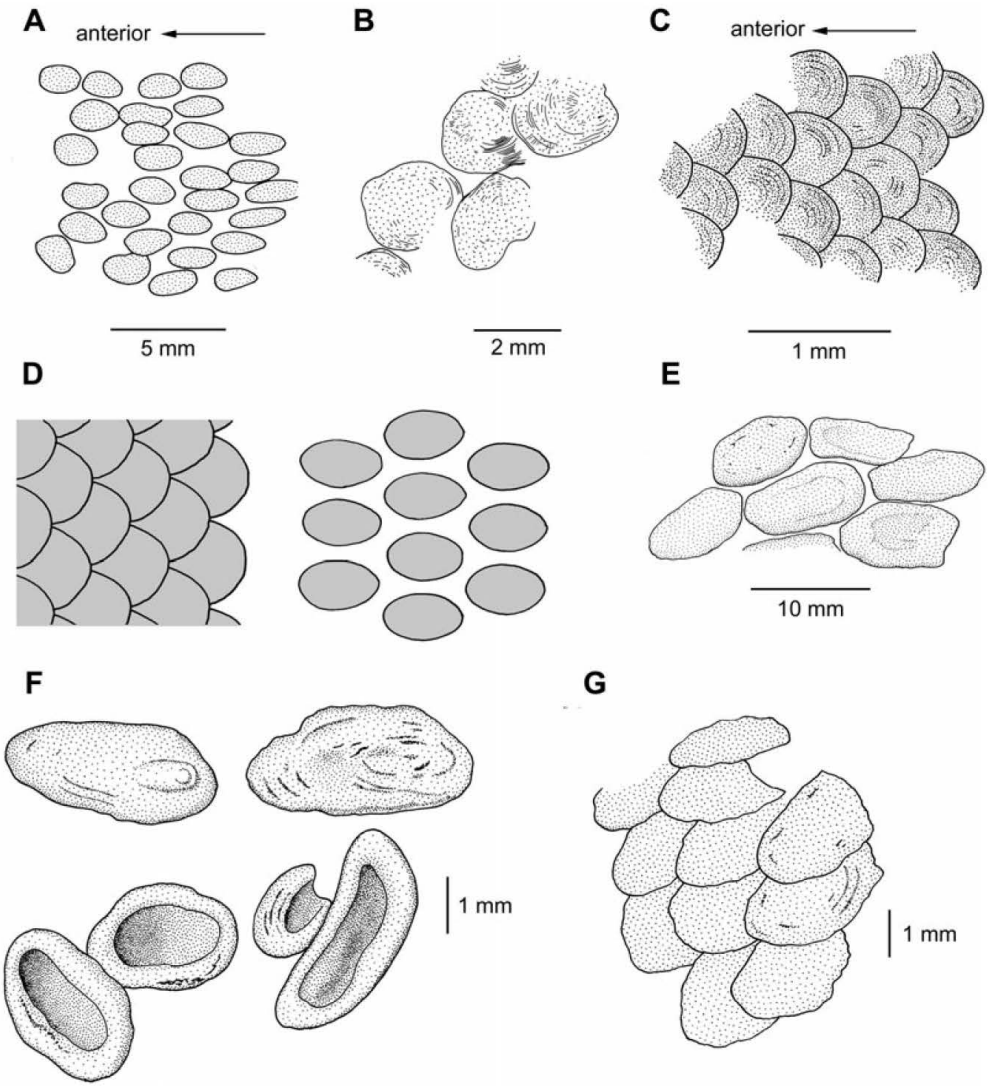

Figure 6. Dorsal scales. A, B, *Archegosaurus decheni*, MB.Am.273. A, scales of the flanks in the region of the ilium. B, scales of the tail, showing concentric rings and radial striae. C, *Sclerocephalus haeuseri,* MB.Am.1314. Scales of the tail. D, schematic reconstruction of the arrangement of dorsal scales in *Sclerocephalus haeuseri* (left), schematic reconstruction of the arrangement of dorsal scales in the sacral region of *Archegosaurus decheni* (right). E, *Eryops megacephalus*, MCZ 1539 (cast). Scales of the tail. F, H, *Greererpeton burkemorani*. F, CMNH 11233. Dorsal scales in external (above) and internal (below) view. G, CMNH 11219. Dorsal scales showing an imbricating pattern.

are aligned in rows that represent the continuation of the gastral scale rows. Each scale of one row is located posteriorly between two scales of the anterior row, as described above in *Archegosaurus*. Only the anterior part of the tail is preserved in this specimen, on which the dorsal scales are densely arranged and possibly overlap. On the hindlimb, scales half the size of those of the trunk are closely set but do not overlap. In SMNS 90055 (sl 198 mm), only the dorsal scales of the tail are preserved. They exhibit the same pattern of overlap as in the small specimens.

Dendrerpeton sp.

The basal temnospondyl *Dendrerpeton* sp. has round-oval dorsal scales that are distinctly broader than the gastral scales (Carroll, 1967; F. Witzmann, pers. observ.) and possess concentric growth rings (Fig. 4C). According to Colbert (1955) the dorsal scales of *Dendrerpeton* sp. overlap regularly.

Trimerorhachids

The dorsal scales of trimerorhachids have basically the same morphology as their gastral scales described above: they are anteroposteriorly elongate and show regular overlap from anterior to posterior (Colbert, 1955; Chase, 1965; Berman, 1973). In contrast to these authors, Olson (1979) came to different conclusions concerning the nature of dermal ossifications in *Trimerorhachis*. He observed a thick layer of up to more than 20 thin scales (designated by him as osteoderms) within the dermis of an individual. Personal observations of the *Trimerorhachis* specimens stored in MCZ, however, corroborate the findings of Colbert, Case, and Berman, and thus their results will be acknowledged here. Nevertheless, Olson's findings remain puzzling; as he wrote, it cannot be ruled out that they might be the result of shrinking of the integument by desiccation.

Dissorophoids

In micromelerpetontids and branchiosaurids, the dorsal scales exhibit a very similar morphology to the gastral scales (see above), but they are slightly less elongate. They show extensive overlap (Credner, 1886; Boy, 1972). In amphibamids dorsal scales are preserved only in *Eoscopus* (Daly, 1994), and they show regular overlap.

Eryopids

In *Eryops*, trunk and tail are covered by tightly set, but not overlapping, round-oval scales (MCZ 1539; Romer & Witter, 1941). Some of these scales are rounded polygonal rather than oval (Fig. 6E). The scales are arranged in the same way as on the flanks of *Archegosaurus* and the large specimens of *Sclerocephalus*. However, the long axes of the scales are inclined posterodorsally at an angle of approximately 30°. In the closely related *Onchiodon*, dorsal scales are known only from larval specimens. They are round-oval and densely cover the flanks and the back, but do not overlap (Werneburg, 1988); as in *Archegosaurus* and *Sclerocephalus*, comparatively thick cup-shaped dorsal scales are located lateral to the gastral scales (Credner, 1893).

Stereospondylomorpha

Among basal stereospondylomorphs, dorsal scales are present in *C. latirostre* in addition to *A. decheni* and *S. haeuseri* (see above). As in *Archegosaurus* the round-oval scales do not overlap in *C. latirostre*, and there is no point contact between them (ROM 5735, MB.Am.1271, MB.Am.1275).

Dorsal scales are also present in different stereospondyls. Van Hoepen (1915) and Findlay (1968) reported very thin dorsal scales in the rhinesuchid *Uranocentrodon*. Their arrangement is unknown. The capitosauroid *Edingerella* has very small, cup-shaped dorsal scales that are loosely scattered with large spaces between them (Lehman, 1966; Janvier, 1992). In *Wellesaurus* the morphology and arrangement of the dorsal scales probably correspond to its gastral scales described above (R. R. Schoch, pers. comm.), as is also the case in *Paracyclotosaurus davidi*, which bears dorsal, round-oval scales that are irregularly set and are not in contact with each other (Watson, 1958). Among trematosaurids, only *Tertremoides* has non-overlapping, round-oval scales on the dorsal surface of the anterior trunk region (Janvier, 1992) that are arranged in rows similar to *Archegosaurus*.

TEMNOSPONDYLS WITHOUT SCALATION

Reduced (thin) scales are present in the amphibamids *Amphibamus* and *Platyrhinops* (Clack & Milner, 1993), and in the branchiosaurids (Boy, 1987). Among dissorophoids, scales are absent in the Lower Triassic amphibamid *Micropholis* (Schoch & Rubidge, 2005). The excellent state of preservation of the articulated specimens strongly suggests that the lack of scales is not an artifact of preservation, but that this temnospondyl had reduced its scalation completely. The Permo-Carboniferous dissorophids (DeMar, 1968) possess plate-like osteoderms on the dorsal surface of the trunk, but no scales have been found. It is certainly possible that the scales are simply not preserved; however, even articulated specimens of *Dissorophus* show no traces of scales.

Within stereospondylomorph temnospondyls, scales are absent in trematosaurids (Steyer, 2002; Schoch, 2006) and metoposaurids (Dutuit, 1976; Schoch, in press). Because many representatives of these taxa are known from well-preserved articulated skeletons that are devoid of any scales, one can suggest that trematosaurids and metoposaurids had a naked skin. An exception is the trematosaurid *Tertremoides* (see above). Furthermore, no scalation is preserved in the capitosauroid *Mastodonsaurus* (Schoch, 1999). It cannot be stated with certainty that it had reduced scalation, because no articulated specimens are known, and the same applies to the basal stereospondyl *Benthosuchus*, from which many postcranial fragments but no scales have been reported (Bystrow & Efremov, 1940). Also, no scalation is visible in the articulated skeleton of the rhytidosteoid *Siderops* (Warren & Hutchinson, 1983).

PHYLOGENY OF SCALATION IN TEMNOSPONDYLS

To ascertain the plesiomorphic situation in temnospondyls, and to trace the development of scalation in different temnospondyl lineages, the scalation pattern for each taxon is mapped on an existing cladogram of temnospondyls based on Witzmann & Schoch (2006) and Schoch & Milner (2000) (Fig. 7). The numbers represent the following characters: 1, presence of gastral scales arranged in a chevron pattern; 1a, rhombic gastral scales; 1b, spindle-shaped gastral scales; 1c, ovoid gastral scales; 2, dorsal scales overlapping on the trunk; 3, dorsal scales not overlapping on the trunk; 4, complete reduction of scales.

Ingroup

The temnospondyls described above with well-preserved scalation were assigned to the ingroup, and the ontogenetically most advanced stages are considered in each case. In the case of temnospondyls without scales, only those taxa in which the excellent state of preservation of the skeleton suggests that the absence of scales represents a real reduction, and is no artifact of preservation (*Micropholis*, trematosaurids, and metoposaurids), were considered. The comparison of the dorsal scales is admittedly impaired by their poor preservation in many taxa.

Outgroup

The Mississippian stem tetrapod *Greererpeton* is considered as an outgroup, and is supplemented by data derived from the Devonian stem tetrapods *Acanthostega*, *Ichthyostega*, and *Tulerpeton*. *Greererpeton* has rhombic gastral scales arranged in a chevron pattern (Godfrey, 1989; F. Witzmann, pers. observ.), the morphology and articulation of which corresponds to *Platyoposaurus*, *Sclerocephalus*, and *Australerpeton* (Fig. 8). As described by Godfrey (1989), the trunk of *Greererpeton* is covered laterally and on the back with

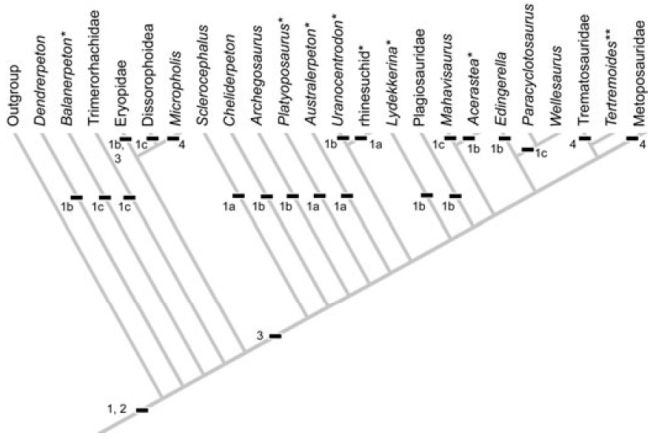

Figure 7. Scalation pattern in temnospondyls mapped on an existing cladogram based on the results of Witzmann & Schoch (2006) and Schoch & Milner (2000). Characters: 1, presence of gastral scales arranged in a chevron pattern; 1a, rhombic gastral scales; 1b, spindle-shaped gastral scales; 1c, ovoid gastral scales; 2, dorsal scales overlapping on the trunk; 3, dorsal scales not overlapping on the trunk; 4, complete reduction of scales. *Taxa in which no dorsal scales are known; **taxa in which no gastral scales are known.

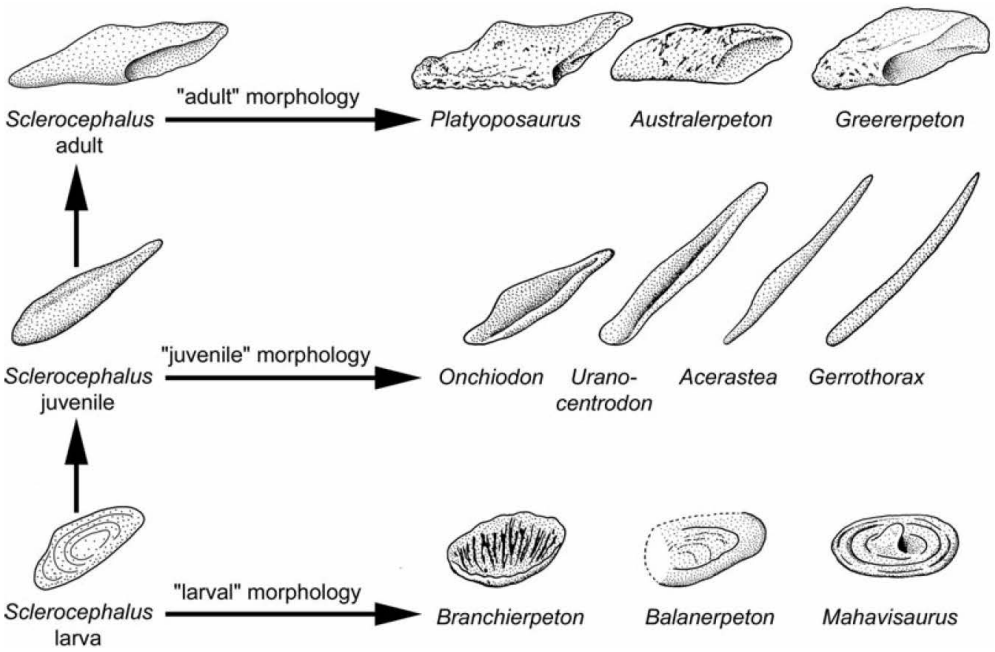

Figure 8. Ontogeny of gastral scales in *Sclerocephalus haeuseri*, and interpretation of the gastral scale morphologies of other temnospondyls and the stem-tetrapod *Greererpeton burkemorani* as 'larval', 'juvenile', and 'adult', respectively. Except for *Sclerocephalus*, the ontogenetically most advanced stages of gastral scales are shown in each case. *Acerastea* redrawn after Warren & Hutchinson (1987), *Australerpeton* redrawn after Dias & Richter (2002), *Balanerpeton* redrawn after Milner & Sequeira (1994), *Branchierpeton* redrawn after Werneburg (1991), *Gerrothorax* redrawn after Nilsson (1946), *Greererpeton* based on CMNH 11073, *Mahavisaurus* redrawn after Janvier (1992), *Onchiodon* redrawn after Credner (1893), *Platyoposaurus* based on PIN 164/1–9, *Sclerocephalus* based on MB.Am.1302, MB.Am.1233, and SMNS 90507, *Uranocentrodon* redrawn after Findlay (1968).

round-oval dorsal scales that overlap regularly from anterior to posterior like a shingled roof (Fig. 6F, G). The dorsal scales are well ossified, internally concave, and externally convex, and some of them bear a medial elevation on the external side as well as concentric growth rings. Scales of this type are also visible on the belly posterior to the last chevron of gastral scales and on the tail (CMNH 11236). The shape of the dorsal scales ranges from almost circular to elongate oval. The resemblance between the thick dorsal scales of *Greererpeton* and the ventrolateral cup-shaped scales of *Archegosaurus*, *Sclerocephalus*, and *Onchiodon* is striking. Also, *Edingerella* and *Tertremoides* have cup-shaped scales, which are, however, smaller and less thick than in *Greererpeton*. It is entirely possible that the thin dorsal scales on the flanks and the back in *Archegosaurus* and *Sclerocephalus* were externally convex and internally concave in the living animal, but were compressed two-dimensionally in the fossil. *Acanthostega* has spindle-shaped gastral scales arranged in a chevron pattern, but round-oval scales are not preserved (Coates, 1996). Thin round-oval scales are known in *Ichthyostega*, which densely covered the tail and the posterior trunk region (Jarvik, 1952). In *Tulerpeton*, thin, round-oval overlapping scales covered the body completely, including the belly (Lebedev & Coates, 1995). There is no clear evidence that the scales on the belly were arranged in a chevron pattern; however, this pattern might be obscured by multiple folding of the skin (O. Lebedev, pers. comm.).

Results

The cladogram illustrates that the presence of gastral scales arranged in a chevron pattern is plesiomorphic for basal tetrapods, and this pattern is highly conservative and retained in different temnospondyl lineages. The only exceptions might be trimerorhachids

and the amphibamid *Eoscopus*, in which it cannot be ascertained if the gastral scales are aligned in a chevron pattern or in transverse rows. In most temnospondyls, the gastral scales are spindle shaped. Only adult *Sclerocephalus*, *Platyoposaurus*, *Australerpeton*, and the rhinesuchid described by Pawley & Warren (2004) have rhombic gastral scales. Ovoid gastral scales are exhibited by *Balanerpeton*, trimerorhachids, and among dissorophoids at least by micromelerpetontids, branchiosaurids, and amphibamids. Furthermore, among stereospondyls, the rhytidosteoid *Mahavisaurus* has ovoid gastral scales, and this is possibly also the case in *Paracyclotosaurus* and *Wellesaurus*.

Regularly overlapping dorsal scales are present in the outgroup (with the exception of *Acanthostega*, in which no dorsal scales are preserved). This is also the case in *Dendrerpeton*, trimerorhachids and – where the dorsal scales are preserved – in dissorophoids. This pattern can be regarded as the plesiomorphic arrangement of dorsal scales in temnospondyls. A reduction of the dorsal scalation took place in different lineages of temnospondyls. Scales appear to be absent in *Micropholis* (Schoch & Rubidge, 2005). Although the dorsal scales are well ossified in eryopids, they are not overlapping. In the basal stereospondylomorph *Sclerocephalus*, the dorsal scales overlap only in the larval and juvenile phase, whereas they are nonoverlapping in the trunk of the adult specimens. From *Cheliderpeton* crownward, the dorsal scales are nonoverlapping in all growth stages. The spindle-shaped or rhombic gastral scales in basal stereospondylomorphs and in rhinesuchid stereospondyls are well ossified, and spindle-shaped gastral scales occur in lydekkerinids, plagiosaurids, and in the rhytidosteoid *Acerastea*. In capitosauroids, spindle-shaped gastral scales can only be demonstrated in *Edingerella* (Janvier, 1992), whereas exclusively round-oval scales have been found in articulated skeletons of *Paracyclotosaurus* and *Wellesaurus*. Scalation was completely lost in trematosaurids and metoposaurids (see above). The reduction probably occurred independently in both groups, as the trematosaurid *Tertremoides* has round-oval dorsal scales at least in the neck region (Janvier, 1992).

DISCUSSION

ONTOGENY OF DERMAL SCALES AND PAEDOMORPHOSIS

The ontogeny of dermal scales can best be traced in *Sclerocephalus* (Fig. 8), because this taxon is represented by an unparalleled, extensive growth series from small larvae to large adults, with skulls ranging from 10 mm to more than 200 mm in length. In small larvae, the gastral scales are arranged in a chevron pattern as they are in large specimens. However, they are distinctly less well ossified and less elongate, so that they resemble the dorsal scales of the flanks and the back. The gastral scales of all temnospondyls – rhombic, spindle-shaped, or ovoid – can probably be traced back to the same type of ventral scales. Furthermore, it can be assumed that dorsal and gastral scales also developed from the same *Anlagen*. This is also supported by the very similar morphology of gastral and dorsal scales in many micromelerpetontids and branchiosaurids (see above). The ovoid gastral scales of larvae become proportionally more elongate in further ontogeny, and attain a spindle-shaped outline in *Sclerocephalus* (Fig. 8). The rhombic morphology of gastral scales in the largest *Sclerocephalus* represents the ontogenetically most advanced condition (i.e. the highest degree of ossification) and can be designated as 'adult'. Accordingly, the very similar rhombic gastral scales of *Platyoposaurus* and *Australerpeton* must have developed ontogenetically from the spindle-shaped 'juvenile' morphology. The rhombic outline is in particular the result of an expansion of the sharp anterodorsal crest that borders the dorsal groove anteriorly (Figs 4B, 5A, B). This crest underwent accelerated growth in an anterodorsal direction and became deeper than the broader, bulge-like crest that limits the dorsal groove posteriorly. The expanded anterior crest overlaps the internal surface of the posterior part of the adjacent scale of the preceding chevron, so that the chevrons overlap anteroposteriorly in ventral view (Fig. 5D). The dorsal groove, which was almost smooth in the spindle-shaped scales, becomes a well-defined dorsolateral facet, the lateral portion of which is slightly convex (most pronounced in *Platyoposaurus*), and the medial portion of which is distinctly concave. As described for *Archegosaurus* above, the ventromedial side of each spindle-shaped gastral scale bears a slightly concave area between an anterior and a posterior ridge (Fig. 4A). During subsequent ontogeny this area differentiated into the well-defined ventromedial facet of the rhombic scale, the contours of which are complementary to the above-described dorsomedial facet. Thus, the convex part of the ventromedial facet fits closely into the concave part of the dorsolateral facet. In *Platyoposaurus*, a sharp crest is developed on the convex part of the ventromedial facet that fits into a corresponding depression on the dorsolateral facet of the adjacent scale. However, most temnospondyls retain the 'juvenile' gastral scale morphology of the slender, spindle-shaped outline, and do not attain the 'adult' rhombic condition, which is interpreted as a paedomorphic trait (Figs 7, 8). This also holds true for the large-growing, well-ossified *Eryops* (MCZ 1738) and the giant rhinesuchid *Uranocentrodon* (Findlay, 1968), the gastral scales of which have the largest absolute size of all temnospondyls

(30–40 mm in length), but nevertheless retain a spindle-shaped morphology. The basal temnospondyl *Balanerpeton* (Milner & Sequeira, 1994) and many dissorophoids maintain the less ossified, ovoid 'larval' morphology of gastral scales, as do the gastral scales of *Mahavisaurus* (Janvier, 1992) (Figs 7, 8).

FUNCTIONAL ASPECTS

Protection and strengthening of the trunk

Romer (1956), Findlay (1968), and Claessens (2004) suggested that the well-ossified gastral scales of early tetrapods and temnospondyls served as protection while crawling on the ground. However, apart from one Devonian trackway (Warren & Wakefield, 1972), no tetrapod trackway from the Palaeozoic and Mesozoic shows clear evidence of a body trace, except for tail drags (Haubold, 1971; Fichter, 1983), indicating that basal tetrapods walked with their bodies supported clear from the ground. Therefore, the gastral scalation was less likely to have served as protection against abrasion during locomotion (moreover the scales were deeply embedded in the dermis, see above), but rather as protection of the viscera from compression while lying on the substrate (R. Holmes, pers. comm.).

The mode of articulation of the spindle-shaped gastral scales allowed telescoping of the scales within the rows during sidewards flexion of the body, and would also accommodate inwards movement of the abominal wall if basal tetrapods exhaled by contraction of the transverse abdominis muscle. Comparison with extant amphibians suggests that this mode of exhalation was already used by basal tetrapods (Brainerd & Monroy, 1998). The combination of protection and flexibility, like that of a 'chain-mail shirt', is a possible explanation for the retention of the 'juvenile' spindle-shaped morphology in most temnospondyls.

In contrast to the spindle-shaped gastral scales, the mode of articulation by indentation between the dorsolateral and ventromedial facets reduced the flexibility between the rhombic gastral scales. This applies especially to the anterior half of the trunk where the scales are more highly ossified. The development of rhombic gastral scales in large specimens of *Sclerocephalus* might be regarded in the context of the mode of swimming. *Sclerocephalus* was a superficially crocodile-like aquatic predator with a long and deep swimming tail. In extant crocodiles, the trunk is stiffened by the osteoderms, the gastralia, and the hypaxial musculature (von Wettstein, 1937). In combination with the long, powerful swimming tail, the stiffened trunk enables crocodiles to accelerate rapidly in water towards prey (Troxell, 1925). Similarly the rhombic scalation might have stabilized the trunk in large individuals of *Sclerocephalus*, supported by the conspicuous uncinate processes on the ribs in the anterior trunk region. The corresponding gastral scalation and the hook-like uncinate processes in *Platyoposaurus* (Konzhukova, 1955) and *Australerpeton* (Dias & Schultz, 2003) probably had a similar effect in these piscivorous predators. In the smaller individuals (known only from *Sclerocephalus*) with a more flexible scalation of spindle-shaped scales, uncinate processes were smaller or absent, and these animals might have performed a more axial mode of swimming.

Phylogenetic reduction of scalation

As outlined above, a reduction of scalation – from an overlapping to a nonoverlapping pattern, a decrease in scale thickness, or even a complete loss of the scales – took place independently in different groups of temnospondyls. Among dissorophoids, the scales became thinner in derived representatives of micromelerpetontids and branchiosaurids, as well as in amphibamids, and they were completely reduced in *Micropholis*. This might be connected with the increasing importance of cutaneous respiration in these small forms (Boy, 1993).

A reduction of scalation also took place among stereospondylomorphs. All basal stereospondylomorphs and rhinesuchid stereospondyls bore well-ossified gastral scales, whereas the scales are often smaller and less ossified or even completely lost in Mesozoic steresopondyls. The Mesozoic stereospondyls were mainly restricted to aquatic habitats, as indicated by the lateral line sulci and the feebly ossified limbs (Schoch & Milner, 2000). Well-ossified gastral scales for protection of the belly (see above) can be expected in temnospondyls that touched the substrate frequently, either in water or on land. Metoposaurid and trematosaurid stereospondyls, which were probably active swimmers and preyed in the open water (Hunt, 1993; Schoch & Milner, 2000; Steyer, 2002), were devoid of gastral scales. The loss of scales provided more freedom of movement for an axial type of locomotion, similar to many fish (Böss, 1982). The need for greater mobility was obviously more important in pelagic swimmers than the protection of scales. In contrast, capitosauroid stereospondyls were benthic animals rather than active swimmers. Nevertheless, the gastral scalation in at least some capitosauroids consists only of thin ovoid scales or might even be absent. The anatomy of most capitosauroids suggests that they could hardly leave the water (Schoch & Milner, 2000), therefore a well-ossified gastral scalation for protection of the belly and support of the internal organs may not have been required.

On the other hand, it is puzzling that no gastral scales are known in the terrestrial stereospondyl *Sclerothorax*. Instead, nodular osteoderms are preserved

on the top of the neural spines (von Huene, 1932), and it cannot be ruled out that other parts of the body were also covered by these dermal ossifications. The primarily terrestrial stereospondyl *Laidleria* has no scales, but was densely covered by irregularly shaped osteoderms on the back and on the belly (Kitching, 1957). The only aquatic Triassic stereospondyls with dermal armour of osteoderms are the highly derived plagiosaurids (Nilsson, 1946; Hellrung, 2003; F. Witzmann, pers. observ.) and the rhytidosteoid *Acerastea* (Warren & Hutchinson, 1987), which possess plate-like or nodular osteoderms on the ventral side (and on the back in plagiosaurids). Although gastral scalation is present, it is feebly developed as the gastral scales are needle-like, and, at least in the case of plagiosaurids, there is a large interspace between the chevrons. In these Mesozoic taxa, the osteoderms had probably taken over the function of protection of the body. This could also apply to the Late Palaeozoic osteoderm-bearing forms, *Peltobatrachus* and the dissorophids, which were supposedly terrestrial. Although the gastral scales are small and needle-like in *Peltobatrachus* (Panchen, 1959), no scales are preserved in dissorophids (see above).

Inferences for the integument

The spindle-shaped, and especially the well-ossified rhombic, gastral scales indicate that the integument was originally very thick in basal tetrapods and temnospondyls, because the gastral scales were deeply embedded in the dermis, as histological sections have shown (Dias & Richter, 2002). This is also supported by the thick, cup-shaped dorsal scales in *Greererpeton* and several Permo-Carboniferous temnospondyls. The fact that many Triassic temnospondyls have less ossified, thinner gastral and dorsal scales could indicate that the integument has become proportionally thinner in these forms (exceptions are the above mentioned, osteoderm-bearing stereospondyls). This is supported by the fact that aquatic sterespondyls have conspicious, deep lateral line sulci on their skull roofing bones. In contrast, the lateral line sulci of most Palaeozoic temnospondyls are comparatively weakly impressed, and consist of long oval depressions that are sometimes difficult to distinguish from the furrows of the dermal sculpture. For example, the piscivorous Upper Permian stereospondylomorphs *Platyopsaurus* and *Australerpeton*, which possess thick rhombic gastral scales, have poorly developed lateral lines on the dermal skull bones (Bystrow, 1935; Barberena, 1998). One may hypothesize that the lateral lines left only weak traces on the bones because the integument was proportionally thicker, whereas in the forms with the possibly thinner integument the lateral lines came to lie on the surface of the bones.

The possibly thinner skin in many Mesozoic temnospondyls might be related to cutaneous respiration and changes of the oxygen content in the atmosphere. Temnospondyls used the buccal pump mechanism for lung breathing, like extant amphibians, whereas their rib morphology precluded the more effective costal aspiration performed by amniotes (Janis & Keller, 2001). Therefore, it is also possible that large temnospondyls like eryopids and stereospondylomorphs, in spite of their disadvantageous surface area to volume ratio, might have relied on cutaneous respiration as an accessory mode of breathing, especially after the gills had been resorbed. A naked skin devoid of scales is surely more favourable for cutaneous gas exchange. Nevertheless, the presence of scales still allows skin breathing to a notable degree. For example, more than 30% of the oxygen intake is processed via the skin in the scaly Reed-Fish (*Erpetoichthys calabaricus*) and the sea-snake *Pelamis platurus* (Feder & Burggren, 1985). Because the bony scales of temnospondyls were located in the dermis, blood capillaries could have spread in the dermal layers and in the epidermis above the scales. Furthermore, it is important to consider that different geochemical models indicate a distinctly higher atmospheric oxygen level during the Carboniferous until the Mid-Permian than is present today, accompanied by a low carbon dioxide level (Graham *et al.*, 1997). This surely considerably facilitated oxygen uptake and carbon dioxide release via the skin in Palaeozoic temnospondyls. In the Upper Permian, the oxygen level of the atmosphere decreased and reached a minimum in the Lower Triassic (Graham *et al.*, 1997). The possibly proportionately thinner integument of many Mesozoic temnospondyls (and the reduction of scales in some forms) might have enhanced the effectiveness of cutaneous respiration in the oxygen-poorer atmosphere, as compared with the Palaeozoic forms with heavily ossified scales within a possibly thicker integument.

CONCLUSIONS

Most temnospondyls exhibit a paedomorphic morphology with respect to the gastral scales, probably driven by the need for a greater flexibility of the trunk. The coupling with the somatic development was decelerated compared with the ancestral situation in many temnospondyls, resulting in the retention of the 'juvenile' spindle-shaped morphology in large adults. In miniaturized forms, like small dissorophoids, the development of the scales was truncated at an early stage so that the scales remained thin and ovoid in outline.

The scalation was reduced independently in different temnospondyl lineages, especially in Mesozoic clades. The thinner scales in Mesozoic stereospondyls

could indicate a relatively thinner integument than in many Palaeozoic temnospondyls, which agrees with their much more conspicuous lateral line sulci. This might have resulted in an increased ability for cutaneous respiration.

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REFERENCES

Barberena MC. 1998. *Australerpeton cosgriffi* n.g., n.sp., a Late Permian Rhinesuchoid amphibian from Brasil. *Anais Da Academia Brasileira de Ciências* **70:** 125–137.

Baur G. 1889. *Palaeohatteria* Credner, and the Proganosauria. *American Journal of Science* **37:** 310–313.

Berman DS. 1973. A trimerorhachid amphibian from the Upper Pennsylvanian of New Mexico. *Journal of Paleontology* **47:** 932–945.

Böss H-P. 1982. Locomotion and feeding in Mesozoic durophagous fishes. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **163/164:** 167–171.

Boy JA. 1972. Die Branchiosaurier (Amphibia) des saarpfälzischen Rotliegenden (Unter-Perm, SW-Deutschland). *Abhandlungen Des Hessischen Landesamtes für Bodenforschung* **65:** 1–137.

Boy JA. 1978. Die Tetrapodenfauna (Amphibia, Reptilia) des saarpfälzischen Rotliegenden (Unter-Perm; SW-Deutschland). 1. *Branchiosaurus*. *Mainzer Geowissenschaftliche Mitteilungen* **7:** 27–76.

Boy JA. 1986. Studien über die Branchiosauridae (Amphibia: Temnospondyli). 1. Neue und wenig bekannte Arten aus dem mitteleuropäischen Rotliegenden (?oberstes Karbon bis unteres Perm). *Paläontologische Zeitschrift* **60:** 131–166.

Boy JA. 1987. Studien über die Branchiosauridae (Amphibia: Temnospondyli; Ober-Karbon – Unter-Perm) 2. Systematische Übersicht. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **174:** 75–104.

Boy JA. 1988. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstes Karbon-Perm). 1. *Sclerocephalus*. *Paläontologische Zeitschrift* **62:** 107–132.

Boy JA. 1993. Synopsis of the tetrapods from the Rotliegend (Lower Permian) in the Saar-Nahe Basin (SW-Germany). *Pollichia Buch* **29:** 155–169.

Brainerd EL, Monroy JA. 1998. Mechanics of lung ventilation in a large aquatic salamander, *Siren lacertina*. *Journal of Experimental Biology* **201:** 673–682.

Broili F. 1926. Über *Sclerocephalus Häuseri* Goldfuss. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung* **1926:** 199–222.

Broili F. 1927. Über die Hautbedeckung der Archegosauridae und Actinodontidae. *Zeitschrift der Deutschen Geologischen Gesellschaft* **79:** 375–384.

Broili F, Schröder J. 1937. Beobachtungen an Wirbeltieren der Karooformation. 26. Über *Lydekkerina* Broom. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung* **1937:** 39–57.

Bystrow AP. 1935. Morphologische Untersuchungen der Deckknochen des Schädels der Stegocephalen. 1. Mitteilung. Schädel der Stegocephalen. *Acta Zoologica* **16:** 65–141.

Bystrow AP, Efremov IA. 1940. *Benthosuchus sushkini* Efremov. A labyrinthodont from the Eotriassic of Sharzenga River. *Trudy Paleontologicheskogo Instituta* **10:** 1–152 (in Russian).

Carroll RL. 1967. Labyrinthodonts from the Joggins Formation. *Journal of Paleontology* **41:** 111–142.

Case EC. 1935. Description of a collection of associated skeletons of *Trimerorhachis*. *Contributions from the Museum of Paleontology, University of Michigan* **4:** 227–274.

Castanet J, Francillon-Vieillot H, de Ricqlès A, Zylberberg L. 2003. The skeletal histology of the Amphibia. In: Heatwole H, Davies M, eds. *Amphibian Biology*, Vol. 5 *Osteology*. Chipping Norton: Surrey Beatty & Sons, 1598–1683.

Chase JN. 1965. *Neldasaurus wrightae*, a new rhachitomous labyrinthodont from the Lower Permian. *Bulletin of the Museum of Comparative Zoology Harvard University* **133:** 156–225.

Clack JA, Milner AR. 1993. *Platyrhinops* from the Upper Carboniferous of Linton and Nýřany and the family Amphibamidae (Amphibia: Temnospondyli). *Pollichia Buch* **29:** 185–191.

Claessens LPAM. 2004. Dinosaur gastralia; origin, morphology, and function. *Journal of Vertebrate Paleontology* **24:** 89–106.

Coates MI. 1996. The Devonian tetrapod *Acanthostega gunnari* Jarvik: postcranial anatomy, basal tetrapod relationships and patterns of skeletal evolution. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **87:** 363–421.

Colbert EH. 1955. Scales in the Permian amphibian *Trimerorhachis*. *American Museum Novitates* **1740:** 1–17.

Cope ED. 1877. Descriptions of extinct vertebrata from the Permian and Triassic Formations of the United States. *Proceedings of the American Philosophical Society* **17:** 182–195.

Cope ED. 1878. Descriptions of extinct Batrachia and Reptilia from the Permian Formations of Texas. *Proceedings of the American Philosophical Society* **17:** 505–530.

Credner H. 1881. Die Stegocephalen aus dem Rotliegenden

des Plauen'schen Grundes bei Dresden. Zweiter Theil. *Zeitschrift der Deutschen Geologischen Gesellschaft* **33:** 574–603.

Credner H. 1886. Die Stegocephalen aus dem Rotliegenden des Plauen'schen Grundes bei Dresden. Sechster Theil. *Zeitschrift der Deutschen Geologischen Gesellschaft* **38:** 576–633.

Credner H. 1893. Die Stegocephalen aus dem Rotliegenden des Plauen'schen Grundes bei Dresden. Zehnter Theil. *Zeitschrift der Deutschen Geologischen Gesellschaft* **45:** 639–704.

Daly E. 1994. The Amphibamidae (Amphibia, Temnospondyli), with a description of a new genus from the Upper Pennsylvanian of Kansas. *University of Kansas Museum of Natural History, Miscellaneous Publication* **85:** 1–59.

DeMar R. 1968. The Permian labyrinthodont amphibian *Dissorophus multicinctus*, and adaptations and phylogeny of the family Dissorophidae. *Journal of Paleontology* **42:** 1210–1242.

Dias EV, Richter M. 2002. On the squamation of *Australerpeton cosgriffi* Barberena, a temnospondyl amphibian from the Upper Permian of Brazil. *Anais Da Academia Brasileira de Ciências* **74:** 477–490.

Dias EV, Schultz CL. 2003. The first Paleozoic temnospondyl postcranial skeleton from South America. *Revista Brasileira de Paleontologia* **6:** 29–42.

Dutuit JM. 1976. Introduction a l'etude paleontologique du Trias continental marocain. Description des premiers stegocephales recueillis dabs le couloir d'Argana (Atlas occidental). *Memoires Du Museum National d'Histoire Naturelle, Paris, Série C* **36:** 1–253.

Feder ME, Burggren WW. 1985. Cutaneous gas exchange in vertebrates: design, patterns, control and implications. *Biological Reviews* **60:** 1–45.

Fichter J. 1983. Tetrapodenfährten aus dem saarpfälzischen Rotliegenden (?Ober-Karbon – Unter-Perm; SW-Deutschland), Teil I: Fährten der Gattungen *Saurichnites*, *Limnopus*, *Amphisauroides*, *Protritonichnites*, *Gilmoreichnus*, *Hyloidichnus* und *Jacobiichnus*. *Mainzer Geowissenschaftliche Mitteilungen* **12:** 9–121.

Findlay GH. 1968. On the structure of the skin in *Uranocentrodon (Rhinesuchus) senekalensis* van Hoepen. *Palaeontologia Africana* **11:** 15–22.

Fraas E. 1896. Die schwäbischen Triassaurier nach dem Material der Kgl. *Naturalien-Sammlung in Stuttgart Zusammengestellt*. Stuttgart: Schweitzerbart.

Fritsch A. 1877. Über einen neuen Saurier aus den Kalksteinen der Permformation (U. Dyas) aus Braunau in Böhmen. *Verlag der königlich-böhmischen Gesellschaft der Wissenschaften* **1877:** 1–3.

Fritsch A. 1883. *Fauna der Gaskohle und der Kalksteine der Permformation Bömens*, Vol. 1. Prague: Selbstverlag.

Fritsch A. 1889. *Fauna der Gaskohle und der Kalksteine der Permformation Bömens*, Vol. 2. Prague: Selbstverlag.

Godfrey SJ. 1989. The postcranial skeletal anatomy of the Carboniferous tetrapod *Greererpeton burkemorani* Romer 1969. *Philosophical Transactions of the Royal Society of London B* **323:** 75–133.

Goldfuss GA. 1847. *Beiträge zur vorweltlichen Fauna des Steinkohlengebirges*. Bonn: Naturhistorischer Verein für die preussischen Rheinlande.

Graham JB, Aguilar N, Dudley R, Gans C. 1997. The Late Paleozoic atmosphere and the ecological and evolutionary physiology of tetrapods. In: Sumida S, Martin KLM, eds. *Amniote Origins: Completing the Transition to Land*. San Diego: Academic Press, 141–167.

Gregory JT. 1950. Tetrapods of the Pennsylvanian nodules from Mazon Creek, Illinois. *American Journal of Science* **248:** 833–873.

Haubold H. 1971. Ichnia Amphibiorum et Reptiliorum fossilum. In: Kuhn O, ed. *Handbuch der Paläoherpetologie*, Vol. 18. Jena: VEB Gustav Fischer Verlag, 1–124.

Hellrung H. 2003. *Gerrothorax pustuloglomeratus*, ein Temnospondyle (Amphibia) mit knöcherner Branchialkammer aus dem Unteren Keuper von Kupferzell (Süddeutschland). *Stuttgarter Beiträge Zur Naturkunde B* **330:** 1–130.

Howes GB, Swinnerton HH. 1901. On the development of the skeleton of the Tuatara, *Sphenodon punctatus* with remarks on the egg, on the hatching and on the hatched young. *Transactions of the Zoological Society of London* **16:** 1–86.

von Huene F. 1932. Ein neuartiger Stegocephalen-Fund aus dem oberhessischen Buntsandstein. *Paläontologische Zeitschrift* **14:** 200–229.

Hunt AP. 1993. Revision of the Metoposauridae (Amphibia: Temnospondyli) and description of a new genus from western North America. *Bulletin of the Museum of Northern Arizona* **59:** 67–97.

Jaekel O. 1896. Die Organisation von *Archegosaurus*. *Zeitschrift der Deutschen Geologischen Gesellschaft* **3:** 505–521.

Janis CM, Keller JC. 2001. Modes of ventilation in early tetrapods: Costal aspiration as a key feature of amniotes. *Acta Palaeontolgica Polonica* **46:** 137–170.

Janvier P. 1992. Les écailles des Trématosaures (Tetrapoda, Temnospondyli): nouvelles données sur les Trématosaures du Trias inférieur de Madagascar. *Bulletin Du Musée National d'Histoire Naturelle, Paris, 4e Série* **14:** 3–13.

Jarvik E. 1952. On the fish-like tail in the ichthyostegid stegocephalians with descriptions of a new stegocephalian and a new crossopterygian from the Upper Devonian of East Greenland. *Meddelelser Om Grønland* **114:** 1–90.

Jordan H. 1849. Ergänzende Beobachtungen zu der Abhandlung von Goldfuss über die Gattung *Archegosaurus*. *Verhandlungen Des Naturhistorischen Vereins für Rheinlande und Westphalen* **6:** 76–81.

Kitching JW. 1957. A small stereospondylous labyrinthodont from the Triassic beds of South Africa. *Palaeontologia Africana* **5:** 67–82.

Konzhukova ED. 1955. *Platyops stuckenbergi* Trautschold – an archegosaurid from the lower zone of the Upper Permian in the Ural region. *Trudy Paleontologichesko Instituta* **49:** 89–127 (in Russian).

Lebedev OA, Coates MI. 1995. The postcranial skeleton of the Devonian tetrapod *Tulerpeton curtum* Lebedev. *Zoological Journal of the Linnean Society* **114:** 307–348.

Lehman JP. 1966. Nouveaux Stégocéphales de Madagascar. *Annales de Paléontologie (Vertébrés)* **52:** 117–139.

von Meyer H. 1858. Reptilien aus der Steinkohleformation in Deutschland. *Palaeontographica* **6:** 59–219.

Milner AR, Sequeira SEK. 1994. The temnospondyl amphibians from the Viséan of East Kirkton, West Lothian, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **84:** 331–361.

Nilsson T. 1946. A new find of *Gerrothorax rhaeticus* Nilsson, a plagiosaurid from the Rhaetic of Scania. *Lunds Universitets Årsskrift, Ny Följd* **42:** 1–43.

Olson EC. 1979. Aspects of the biology of *Trimerorhachis* (Amphibia: Temnospondyli). *Journal of Paleontology* **53:** 1–17.

Panchen A. 1959. A new armoured amphibian from the Upper Permain of East Africa. *Philosophical Transactions of the Royal Society of London B* **242:** 207–281.

Pawley K, Warren AA. 2004. Immaturity vs paedomorphism: a rhinesuchid stereospondyl postcranium from the Upper Permian of South Africa. *Palaeontologia Africana* **40:** 1–10.

Pawley K, Warren AA. 2005. A terrestrial temnospondyl from the Lower Triassic of South Africa: The postcranial skeleton of *Lyddekerina huxleyi* (Amphibia: Temnospondyli). *Palaeontology* **48:** 281–298.

Romer AS. 1956. *Osteology of the Reptiles*. Chicago: University of Chicago Press.

Romer AS. 1969. A temnospondylous labyrinthodont from the Lower Carboniferous. *Kirtlandia* **6:** 1–20.

Romer AS, Witter RV. 1941. The skin of the rhachitomous amphibian *Eryops*. *American Journal of Sciences* **239:** 822–824.

Ruibal R, Shoemaker V. 1984. Osteoderms in anurans. *Journal of Herpetology* **18:** 313–328.

Schoch RR. 1999. Comparative osteology of *Mastodonsaurus giganteus* (Jaeger, 1828) from the Middle Triassic (Lettenkeuper: Longobardian) of Germany (Baden-Württemberg, Bayern, Thüringen). *Stuttgarter Beiträge Zur Naturkunde B* **278:** 1–173.

Schoch RR. 2003. Early larval ontogeny of the Permo-Carboniferous temnospondyl *Sclerocephalus*. *Palaeontology* **46:** 1055–1072.

Schoch RR. 2006. A new trematosaurid amphibian from the Middle Triassic of Germany. *Journal of Vertebrate Paleontology* **26:** 29–43.

Schoch RR. in press. A new stereospondyl from the Lower Keuper of Germany and the origin of the Metoposauridae. *Zoological Journal of the Linnean Society* in press.

Schoch RR, Milner AR. 2000. Stereospondyli. In: Wellnhofer P, ed. *Handbuch der Paläoherpetologie*, Vol. 3B. Munich: Verlag Dr Friedrich Pfeil, 1–203.

Schoch RR, Rubidge BS. 2005. The amphibamid *Micropholis* from the *Lystrosaurus* Assemblage Zone of South Africa. *Journal of Vertebrate Paleontology* **25:** 502–522.

Steen MC. 1931. The British Museum collections of Amphibia from the Middle Coal Measures of Linton, Ohio. *Proceedings of the Zoological Society London B* **1930:** 849–891.

Steyer JS. 2002. The first articulated trematosaur 'amphibian' from the Lower Triassic of Madagascar: implications for the phylogeny of the group. *Palaeontology* **45:** 771–793.

Trautschold H. 1884. Die Reste permischer Reptilien des Paläontologischen Kabinets der Universität Kasan. *Nouveaux Mémoires de la Société Impériale Des Naturalistes de Moscou* **15:** 1–38.

Troxell EL. 1925. Mechanics of crocodile vertebrae. *Bulletin of the Geological Society of America* **36:** 605–614.

Van Hoepen ECN. 1915. Stegocephalia of Senekal, O.F.S. *Annals of the Transvaal Museum* **5:** 124–149.

Voeltzkow A, Döderlein L. 1901. Beiträge zur Entwicklungsgeschichte der Reptilien III. Zur Frage nach der Bildung der Bauchrippen. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **26:** 313–336.

Warren AA, Hutchinson MN. 1983. The last labyrinthodont? A new brachyopoid (Amphibia, Temnospondyli) from the Early Jurassic Evergreen Formation of Queensland, Australia. *Philosophical Transactions of the Royal Society of London B* **303:** 1–62.

Warren AA, Hutchinson MN. 1987. The skeleton of a new hornless rhytidosteid (Amphibia, Temnospondyli). *Alcheringa* **11:** 291–302.

Warren AA, Wakefield NA. 1972. Trackways of tetrapod vertebrates from the Upper Devonian of Victoria, Australia. *Nature* **238:** 469–470.

Watson DMS. 1958. A new labyrinthodont (*Paracyclotosaurus*) from the Upper Trias of New South Wales. *Bulletin of the British Museum of Natural History, Geology* **3:** 233–263.

Werneburg R. 1987. Dissorophoiden (Amphibia, Rhachitomi) aus dem Westphal D (Oberkarbon) der ČSSR. *Branchiosaurus salamandroides* Fritsch 1876. *Zeitschrift für Geologische Wissenschaften* **15:** 681–690.

Werneburg R. 1988. Die Amphibienfauna der Oberhöfer Schichten (Unterrotliegendes, Unterperm) des Thüringer Waldes. *Veröffentlichungen Naturhistorisches Museum Schleusingen* **3:** 2–27.

Werneburg R. 1991. Die Branchiosaurier aus dem Unterrotliegend des Döhlener Beckens bei Dresden. *Veröffentlichungen Naturhistorisches Museum Schleusingen* **6:** 75–99.

Werneburg R. 1994. Dissorophoiden (Amphibia, Rhachitomi) aus dem Westphal D (Oberkarbon) von Böhmen – *Limnogyrinus elegans* (Fritsch 1876). *Zeitschrift für Geologische Wissenschaften* **22:** 457–466.

Werneburg R, Steyer JS. 2002. Revision of *Cheliderpeton vranyi* Fritsch, 1877 (Amphibia, Temnospondyli) from the Lower Permian of Bohemia (Czech Republic). *Paläontologische Zeitschrift* **76:** 149–162.

von Wettstein O. 1937. 2. Ordnung der Klasse Reptilia: Crocodilia. In: Krumbach T, ed. *Handbuch der Zoologie. Eine Naturgeschichte der Stämme Des Tierreichs.*, Vol. 7. Berlin: de Gruyter, 234–424.

Witzmann F, Schoch RR. 2006. The postcranium of *Archegosaurus decheni*, and a phylogenetic analysis of temnospondyl posterania. *Palaeontology* **49:** 1211–1235.

Zylberberg L, Wake MH. 1990. Structure of the scales of *Dermophis* and *Microcaecilia* (Amphibia: Gymnophiona), and a comparison to dermal ossifications of other vertebrates. *Journal of Morphology* **206:** 25–43.

Structure of dermal scales in early tetrapods and tetrapodomorph fishes

Appendix 9

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Morphological and histological changes of dermal scales during the fish-to-tetrapod transition

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Abstract

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The gastral scales of limbed tetrapodomorphs evolved from the 'elpistostegid'-type of scale by an enlargement and differentiation of the articulation facets and a shortening and broadening of the keel. These changes caused a tighter connection between gastral scales within a scale row and a greater overlap between the rows. Dorsal round scales of limbed tetrapodomorphs developed from a gastral scale-type by an alteration of the ontogenetic pathway. The posterolateral direction of scale rows in 'elpistostegids' was retained in the gastral scalation of most limbed tetrapodomorphs, whereas the arrangement of round dorsal scales is modified to a transverse orientation. Both gastral and dorsal scales of limbed tetrapodomorphs consist solely of parallel-fibred bone with circumferential growth marks. The proportionally larger overlap surfaces of gastral scales and their mode of articulation in the ventral midline indicate that the body of limbed tetrapodomorphs might have been more flexible than that of their finned relatives. The alteration of dermal scales was one of the most rapid morphological changes during the fish-to-tetrapod transition. Once established, gastral and dorsal scales were retained as a conservative character in different lineages of basal tetrapods, in both the amphibian and the amniote lineages.

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Introduction

In recent years, numerous new finds of Devonian limbed tetrapodomorphs (stem-tetrapods) and their fish-like relatives have considerably increased our knowledge about these animals and have challenged our view of the fish-to-tetrapod transition and early tetrapod evolution. This applies especially to the evolution of limbs (Coates and Clack 1990; Boisvert 2005; Shubin *et al.* 2006; Boisvert *et al.* 2008; Clack 2009), modification of skull and visceral skeleton (Coates and Clack 1991; Clack 1992, 1998, 2002; Clack *et al.* 2003; Brazeau and Ahlberg 2006; Daeschler *et al.* 2006; Downs *et al.* 2008), the vertebral column (Ahlberg *et al.* 2005) as well as the palaeoecology of the earliest limbed vertebrates (e.g. Coates and Clack 1995; Schultze 1997; Clack 2006; Niedźwiedzki *et al.* 2010). In contrast, the question of how the skin was affected during the fish-to-tetrapod transition is still largely unexplored. Although the soft parts of the skin are usually not preserved in vertebrate fossils, the mineralised elements that were formed within the dermis are often well preserved and can be used as good osteological correlates for the skin structure. As the integument determines several aspects of a vertebrate's metabolism and mode of life, a better knowledge of this structure in finned and limbed tetrapodomorphs will contribute to our understanding of the transition from fish-to-tetrapod.

Since the pioneering works of Meyer (1858), Fritsch (1883, 1889), Credner (1881, 1886, 1893) and Cope (1884), it is well established that stem- and basal tetrapods did not possess a naked skin, but rather had the potential to form various types of dermal ossifications. Stem-tetrapods and most Palaeozoic basal tetrapods were covered by ossified dermal scales, which often resemble those of bony fishes. Meyer (1858) first distinguished two different types of dermal scales in 'labyrinthodonts': rhombic or spindle-shaped scales that form rows arranged in a chevron pattern on the ventral face of the trunk between pectoral and pelvic girdle, and thin round or ovoid scales covering the dorsal portion of the trunk together with flanks, tail and limbs. Our knowledge of dermal

ossifications was later increased by different studies on dermal scales in the Devonian stem-tetrapod *Ichthyostega* (Jarvik 1952), colosteids (Romer 1972; Hook 1983; Godfrey 1989a), lepospondyls (e.g. Bossy and Milner 1998; Carroll 1998a,b,c; Carroll and Andrews 1998) and different temnospondyls (e.g. Broili 1927; Romer and Witter 1941; Colbert 1955; Findlay 1968; Janvier 1992; Boy and Sues 2000; Dias and Richter 2003; for a review of scale morphology and articulation pattern in temnospondyls as well as a full list of references see Witzmann 2007). A study on the histology of basal tetrapod scales has so far only been performed by Dias and Richter (2003), who investigated thin sections of the scales of the basal stereospondyl *Australerpeton*. Apparently, many derived temnospondyls especially of Mesozoic age have partially or completely reduced their dermal scalation (Witzmann 2007).

Apart from dermal scales, some lineages of basal tetrapods possess plate-like ossifications that are generally referred to as osteoderms in the postcranial skeleton (Castanet *et al.* 2003). These osteoderms often possess an irregular outline and may also vary considerably in the mode of articulation. Dissorophid temnospondyls bear osteoderms covering the dorsal spine (e.g. Carroll 1964; DeMar 1966, 1968; Dilkes and Brown 2007; Dilkes 2009), superficially similar to chroniosuchians (Golubev 1998; Novikov *et al.* 2000; Witzmann *et al.* 2008) and to the plagiosaurid *Plagiosuchus* (Witzmann and Soler-Gijón 2010). In temnospondyls, dermal armor of osteoderms covering their entire body was reported in *Peltobatrachus* (Panchen 1959) and the plagiosaurid *Gerrothorax* (Nilsson 1946; Hellrung 2003; Jenkins *et al.* 2008). Histological investigations of basal tetrapod osteoderms were carried out by Witzmann and Soler-Gijón (2010). Olson (1979) reported a puzzling find in one individual of the temnospondyl *Trimerorhachis insignis*. He observed a thick layer of more than 20 thin dermal ossifications consisting of acellular bone, referred to as 'osteoderms' in the skin of this specimen. These ossifications are not in accordance with the scales of trimerorhachids as described by Colbert (1955), Chase (1965), Berman (1973) and Witzmann (2007).

The present study provides an overview on the morphology and arrangement of dermal ossifications referred to as 'scales' as well as their distribution in different clades of stem- and basal tetrapods. It seeks to establish the relationships of these dermal skeletal elements with those found in osteichthyan fishes, especially in finned tetrapodomorphs or 'elpistostegids'. This work demonstrates which alterations occurred in the morphology, histology and arrangement of scales during the fish-to-tetrapod transition, and interprets how and why these changes occurred.

Definition of anatomical terms

Castanet *et al.* (2003) provided a structural distinction between dermal scales and osteoderms in tetrapods: osteoderms are often irregularly shaped plates of dermal bone that usually bear a pitted outer surface; in contrast, dermal scales are thinner than osteoderms, often round or elongate oval in outline that may overlap. In contrast to this definition, Vickaryous and Sire (2009) designated all skeletal elements within the dermis that are principally composed of osseous tissue without odontogenic components (i.e. dentine and/or enamel/enameloid) as osteoderms; they are generally plate-like, but may vary greatly in shape, size, ornamentation and articulation. Following this view, Vickaryous and Sire (2009) referred the scales of finned and limbed tetrapodomorphs like those of the tristichopterid *Eusthenopteron*, 'elpistostegids' or the colosteid *Greererpeton* to as scale-shaped osteoderms, as they have reduced all dental tissue components. These authors regarded gymnophionans as the only tetrapods that bear dermal scales, as the gymnophionan dermal scale possesses a thick basal layer of elasmodine (a plywood-like dentine), structurally similar to the elasmoid scales of most teleosts. Although acceptable as an alternative term, the definition by Vickaryous and Sire (2009) is not as useful from an evolutionary perspective and for comparative studies as that provided by Castanet *et al.* (2003). It appears somewhat arbitrary to link the term 'dermal scale' with the presence of dental tissue. For example, several porolepiform and 'osteolepiform' sarcopterygian taxa secondarily reduced the dental components of their scales, whereas other representatives of both groups did not (Jarvik 1980). It is not logical to designate the dermal skeletal elements of one group as dermal scales, whereas in closely related forms, the same, albeit histologically simplified elements are termed osteoderms. In practice, this designation would lead to an unnecessary confusion. Therefore, the distinction of dermal elements *sensu* Castanet *et al.* (2003) is followed in the present paper.

The ventral scales of stem- and basal tetrapods are termed 'gastral scales' *sensu* Witzmann (2007) rather than 'gastralia', to avoid confusion with the gastralia or 'abdominal ribs' present in several amniotes (Romer 1956; Claessens 2004). The round or ovoid scales covering flanks and back of the trunk, limbs and tail in limbed tetrapodomorphs are referred to as 'round-oval scales'. The scales in finned tetrapodomorphs are simply termed 'ventral scales' or 'dorsal scales'. Similarly orientated scales in finned and limbed tetrapodomorphs that overlap each other along their longitudinal axis are referred to as 'rows' or 'scale rows'. In limbed tetrapodomorphs, two contralateral rows from the same segment articulate in the ventral midline via alternating scales and are called a 'chevron' (see Witzmann 2007). Two posterolaterally aligned rows from opposite sides of the trunk form an anteriorly directed chevron, and two anterolaterally directed rows form a posteriorly directed chevron. In finned tetrapodomorphs, a single longitudinal row of scales is present in the dorsal and ventral midline of the trunk (see below), and therefore, the term 'chevron' is avoided here. The 'scale length' is measured parallel to the scale row axis, the 'scale width' perpendicular to it.

In the present study, analyses by Ruta *et al.* (2003a) and Ruta and Coates (2007) are taken as the phylogenetic framework of tetrapodomorph interrelationships. According to

these analyses, temnospondyls, 'anthracosaurs' and lepospondyls belong to the crown-group Tetrapoda, named 'basal tetrapods' in this study, whereas Devonian limbed vertebrates, colosteids, baphetids, *Crassigyrinus* and whatcheeriids are designated as stem-tetrapods or limbed tetrapodomorphs. For an alternative view of stem-group and crown-group tetrapod relationships, see Laurin and Reisz (1997) and Vallin and Laurin (2004).

Material and Methods

Osteolepis macrolepidotus (Osteolepidae, Mid-Devonian, Orkney, Scotland). MB.f.5324, 5346, 5390: complete specimens in dorsal and ventral view.

Panderichthys rhombolepis ('Elpistostegidae', Mid-Devonian, Latvia). MB.f.104, 1891.1-20: isolated scales; MB.Hi.413, 415, MB.f.1891.3: thin sections of scales; LDM G 60/264: complete fish in ventral view; LDM G 60/123: complete fish with dorsal scalation in ventral view.

Acanthostega gunnari (stem-tetrapod, Late Devonian, Greenland). MGUH 252: gastral scales (housed in Diversity Museum of Zoology, University of Cambridge, UK).

Ichthyostega sp. (stem-tetrapod, Late Devonian, Greenland). MGUH 6/09: tail with scales (housed in Diversity Museum of Zoology, University of Cambridge, UK).

Tulerpeton curtum (stem-tetrapod, Late Devonian, Russia). Collection 2921: several isolated (PIN 2921/3237) and articulated (PIN 2921/3236) dermal scales.

Greererpeton burkemorani (Colosteidae, Visé/Namur, USA). CMNH 11073, 11113, 11713: gastral scales and round-oval dorsal scales.

Colosteus scutellatus (Colosteidae, Westphalian D, USA). AMNH 6917: trunk with dermal scales in dorsal and ventral view.

Sclerocephalus haeuseri (Temnospondyli, Stereospondylomorpha, Early Permian, Germany). MB.Am.1203, 1314: gastral and round-oval scales.

Archegosaurus decheni (Temnospondyli, Stereospondylomorpha, Early Permian, Germany). MB.Am.289: trunk with gastral and dorsal scales.

Plagiosuchus pustuliferus (Temnospondyli, Plagiosauridae, Middle Triassic, Germany). SMNS 84794: gastral scales.

Gerrothorax sp. (Temnospondyli, Plagiosauridae, Middle Triassic, Germany). SMNS 91342: gastral scales with underlying plate-like osteoderms.

Gephyrostegus bohemicus ('Anthracosauria', Gephyrostegidae, Westphalian D, Nýřaný, Czech Republic). MB.Am.719a, b: almost complete specimen with gastral scales; MB.Am.1901.1378a, b: trunk with gastral and dorsal scales.

Thin sections of dermal scales were prepared with a thickness of approximately 30 µm using the standard method of Chinsamy and Raath (1992). The thin sections were examined using a Leica DC 300 polarizing stereomicroscope with transmitted ordinary and polarized light. The terminology of Francillon-Vieillot *et al.* (1990) concerning scale histology is used throughout the text.

Morphological abbreviations

adc, anterodorsal crest; af, anterior facet; alf, anterolateral articulation facet; aos, anterior overlap surface; ar, anterior ridge; bl, basal layer; cf, connecting fibres; cl, bone cell-lacunae; con, concavity; cr, crest; dgr, dorsal groove; dmr, dorsal median scale row; dms, dorsal median scale; dos, dorsal oblique scale row; ds, dorsal scale; eaf, external articulation facet; el, external layer; fl, longitudinally cut fibres; fs, free surface; ft, transversely cut fibres; fur, furrow; GM, growth marks; gr, groove; gs, gastral scale; iaf, internal articulation facet; icl, interclavicle; ISF, interwoven structural fibres; ivs, inversion scale; kl, keel; me, medial end; ml, middle layer; ost, osteoderm; pbc, posterior bulge-like crest; pbc*, developing posterior bulge-like crest; pf, posterior facet; PFB, parallel-fibred bone; plf, posterolateral facet; pr, posterior ridge; PVC, primary vascular canal; ShF, Sharpey's fibres; SO, secondary osteon; tub, tubercles; vmf, ventromedial facet; vmr, ventral median scale row; vms, ventral median scale; vos, ventral oblique scale row.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; CMNH, Cleveland Museum of Natural History, Cleveland/Ohio, USA; LDM, Latvian Museum of Natural History, Riga, Latvia; MB, Museum für Naturkunde, Berlin, Germany; MGUH, Geological Museum, University of Copenhagen, Denmark; PIN, Paleontological Institute and Museum of the Russian Academy of Science, Moscow, Russia; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany.

Results

Morphology of the scales and their arrangement in the finned tetrapodomorph Panderichthys rhombolepis

In order to enable a comparison to scale morphology and arrangement in limbed vertebrates, we describe the morphology and arrangement of the dermal scales covering ventral and dorsal side, as well as the flanks of the trunk of *Panderichthys rhombolepis*. The scales of the paired fins and of the caudal fin of *Panderichthys* are not described in this study, as dermal scales covering extremities and tail in stem- and basal tetrapods are rarely and incompletely preserved and preclude a comparison between taxa.

Dermal sculpture of the scales. The free surface of each scale (i.e. the non-overlapped part of the external surface) bears a dermal sculpture similar to that of the dermal bones of basal tetrapods (Gross 1930, 1966; Vorobyeva and Schultze 1991; Witzmann 2007; Witzmann *et al.* In press). It mostly consists

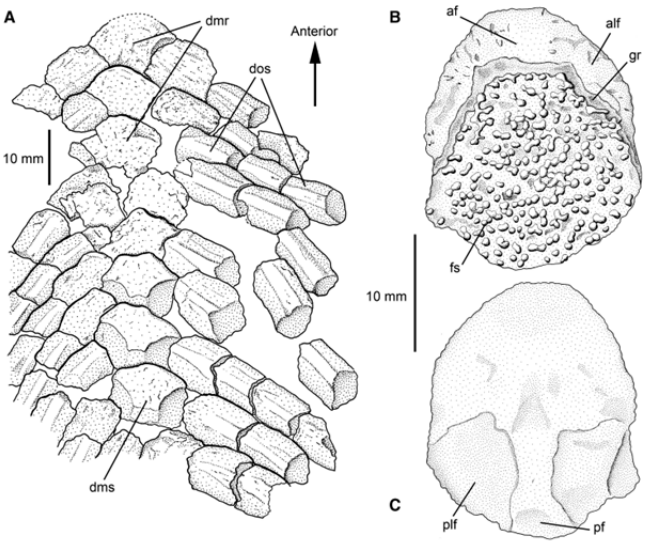

Fig. 1—Scales of *Panderichthys rhombolepis*. —**A.** LDM G 60/123. Dorsal median row of scales with dorsal oblique rows of scales in internal (ventral) view. —**B, C.** MB.f.1891.1. Median ?dorsal scale, (B) external view, (C) internal view.

of bony tubercles (see histology below) that are frequently interconnected by low ridges (Figs. 1, 2). In those parts where these ridges are approximately as high as the tubercles, the sculpture appears vermiculate. The areas between the tubercles and ridges are externally concave and bear several openings of vascular canals.

Dorsal median scale row . On the back of the trunk, a single dorsal median row of roughly hexagonal scales is visible. Lateral to this row, dorsal anteromedially directed rows of scales are visible on both sides, the dorsal oblique scale rows (Fig. 1A). On their external surface, the hexagonal median scales have articulation facets in their anterior and anterolateral portions (Fig. 1B). These facets are separated from the sculptured surface (free surface) by a groove, similar to that described by Jarvik (1948) for osteolepid scales. The anterior facet is overlapped by the posterior portion of the anteriorly neighbouring scale of the median row, resulting in an anteroposterior overlap within the median row (Fig. 1A). The anterolateral facets of the median scales are overlapped by the dorsalmost scale of the left and right dorsal oblique scale rows, respectively, which in turn are overlapped in their dorsal parts by the preceding median scale. On the internal (i.e. ventral) surface of the median scales, the posterior facet that overlaps the anterior portion of the following posterior median scale, as well as the posterolateral facets that overlap the dorsal portion of the dorsalmost scale of one dorsal oblique scale row are clearly visible (Fig. 1A, C).

The dorsal oblique scale rows . The scales of these anteromedially directed rows are roughly rhomboid in outline and generally higher than long (Fig. 2A–C). They are overlapped by dorsally and anteriorly adjoining scales. In external view, each scale has an approximately triangular facet of articulation in its dorsal portion which has often a convex dorsal margin and contributes to approximately one-third of the scale length (Fig. 2A). This external facet of articulation is distinctly depressed and separated from the rest of the scale by a well-defined margin. Its surface is rather smooth with the exception of faint striae along the length of the scale. The facet is overlapped by the dorsally neighbouring scale of the same row. The anterior portion of each scale possesses a rather smooth overlap surface which is overlapped by scales of the adjoining anterior row. This overlapping surface is not as clearly offset from the sculptured free surface of the scale as the external articulation facet described above. It contributes to approximately one-fourth of the scale width. The non-overlapped, sculptured area of the scales appears roughly quadrangular in shape. In internal view, the scales have a rather smooth surface (Fig. 2B). A distinct articulation facet, the internal facet, is visible in the ventral portion and corresponds in outline and size to the external facet. This facet overlaps the dorsal portion of the ventrally adjoining scale of the same row. A distinct ridge or keel extends from the rim of the internal facet towards the longitudinal axis of the scale (i.e. the scale row axis) to its dorsal tip. It is broadly rounded and divides the internal surface of the scale into two unequally sized areas, a smaller anterior and a larger posterior area. This posterior area is more depressed and overlaps the anterior overlapping surface of two scales from the posteriorly neighbouring scale row.

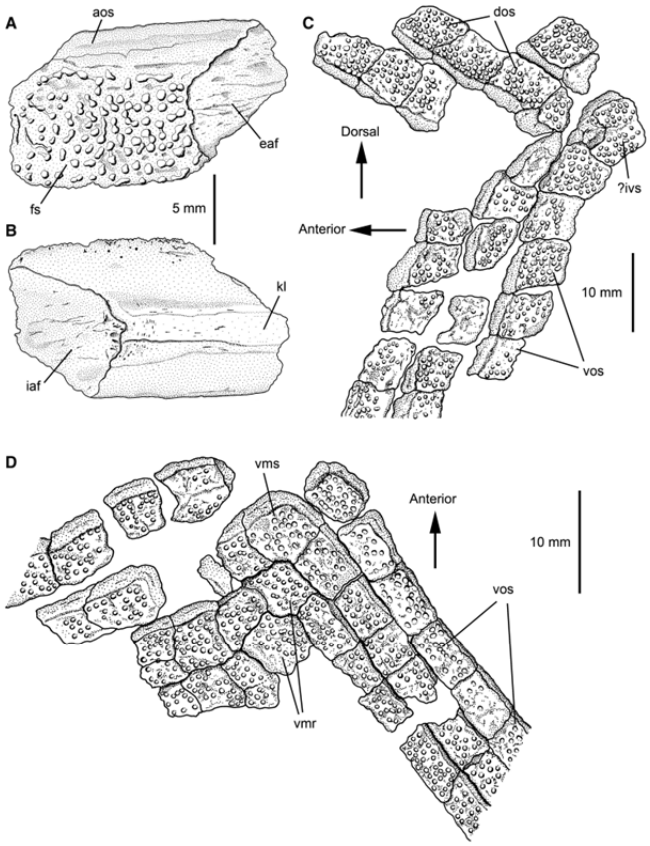

Fig. 2—Scales of *Panderichthys rhombolepis*. —**A, B.** MB.f.1891.4. Rhombic scale, (A) external view, (B) internal view. —**C.** LDM G 60/264. Rhombic scales of the dorsal oblique and the ventral oblique rows in external view, meeting at the ventrolateral part of the trunk. Inversion scales are probably intercalated between the dorsal and ventral rows. —**D.** LDM G 60/264. Scales of the ventral median row in external (ventral) view with ventral oblique rows of scales.

The ventral median scale row . A single row of roughly hexagonal scales corresponds to the dorsal median scale row, which is visible in the ventral midline of the trunk (Fig. 2D). Unfortunately, the ventral median row of scales is not as well preserved as those from the dorsal region. However, some of the median ventral scales are clearly visible, and they basically have the same morphology as the dorsal median scales. The only difference is that they seem to be somewhat smaller than their dorsal counterparts, which has also been described for the median scales of osteolepids (Jarvik 1948).

The ventral oblique scale rows . These rows correspond to the dorsal oblique scale rows covering the dorsal part of the trunk and the lateral flanks. The ventral oblique scale rows extend from the ventral median scale row in a posterolateral direction and cover the ventral face of the trunk (Fig. 2C, D). The scales of these rows possess the same morphology and rhomboid outline as the scales of the dorsolateral transverse scale rows. They are oriented in the way that each scale is overlapped by adjoining scales from anteriorly and ventrally. This means that the triangular external facet is directed anteroventrally (towards the median scale row), and the corresponding internal facet is directed posterodorsally. In other words, the scales from both the dorsal oblique and ventral oblique rows overlap in an anteromedial-posterolateral direction.

The 'ventro-lateral ridge' . Ventral oblique scale rows cover only the ventral face of *Panderichthys* and are thus shorter than dorsal oblique scale rows. Ventral and dorsal rows meet in the ventral surface of the flanks (Fig. 2C), at the same level of the paired fins, along a line called 'ventro-lateral ridge' in osteolepids (Jarvik 1948). In osteolepids, the rows meet at an angle where the dorsalmost scales of the ventral rows articulate directly with the ventralmost scales of the dorsal rows (Jarvik 1948; fig. 26). In *Panderichthys*, however, a roughly pentagonal scale seems to be intercalated between each dorsal and

ventral row (Fig. 2C). Such intercalated scales or 'inversion scales' are also present in certain fossil actinopterygians with rhombic scalation (Jessen 1972). Poor preservation precludes a definite diagnosis for the pattern in *Panderichthys*; however, as the triangular external articulation facets are directed differently in scales from the dorsal and ventral rows, the presence of a specialized 'inversion scale' between them is probable.

The scales of Elpistostege and Tiktaalik

Elpistostege watsoni . Just a few preserved scales from scarce postcranial material of *Elpistostege* were described by Schultze and Arsenault (1985) and Schultze (1996). They basically show the same morphology as those of *Panderichthys*. However, the scales of *Elpistostege* are comparatively longer, at least twice as long as wide. The scales within a row show extensive overlap: both external triangular articulation facet and the corresponding internal facet measure up to half the length of the scale. A distinct keel is present on their internal surface. Similar to *Panderichthys*, there is a narrow anteroposterior overlap between scale rows. The free external surface bears dermal bone sculpture, which, compared with *Panderichthys*, consists to a great extent of bony ridges rather than tubercles.

Tiktaalik rosae . Dermal scales of *Tiktaalik* are similar to those of *Panderichthys*, presenting a rhombic outline and a dermal sculpture of tubercles on their free external surface (Daeschler *et al.* 2006). The scales on the dorsal surface exhibit the arrangement described above for *Panderichthys* (Daeschler *et al.* 2006; fig. 2b), whereas scales on the ventral body surface are not reported. However, there is no compelling argument to assume that they were not present in the living animal.

The scales in Devonian limbed tetrapodomorphs

The Devonian stem-tetrapods (limbed tetrapodomorphs) in which the postcranium and scales are preserved are *Acanthostega*, *Ichthyostega* and *Tulerpeton*, as well as unidentified remains from Red Hill locality, Nevada, USA.

Acanthostega gunnari . This Famennian stem-tetrapod possesses gastral scales on the ventral face of its trunk, as reported by Coates (1996). The morphology and arrangement of these scales resembles closely those of the temnospondyls *Archegosaurus decheni*, *Onchiodon labyrinthicus* and juvenile *Sclerocephalus haeuseri* (Witzmann 2007). Each gastral scale is spindle-shaped in outline, with a tapering medial and a rounded lateral end (Fig. 3A–C). The scales are arranged en-chevron, with the tapering ends being anteromedially directed. On the ventral surface, each gastral scale exhibits two ridges, a distinct posterior and a less distinct anterior one. Both ridges are separated by a slight concavity and become more flattened towards the tapering end of the scale. On the dorsal or internal face, each gastral scale bears an anteroposteriorly asymmetric deep groove, which is posteriorly delimited by a steep, thickened and bulge-like crest, whereas a thin, anterodorsally directed crest delimits the groove anteriorly. This groove gradually shallows towards the tapering (medial) end, but terminates rather abruptly towards the rounded (lateral) end of the gastral scale. The tapering end of each scale fits into the dorsal groove of the medially adjoining scale from the same row (Fig. 3C). Thus, gastral scales from the same row overlap in a posterolateral direction in ventral view and show the same telescoping pattern as in temnospondyls (Witzmann 2007). Both the concave dorsal surface and the ventral side of the scales are smooth without sculpture. The scale

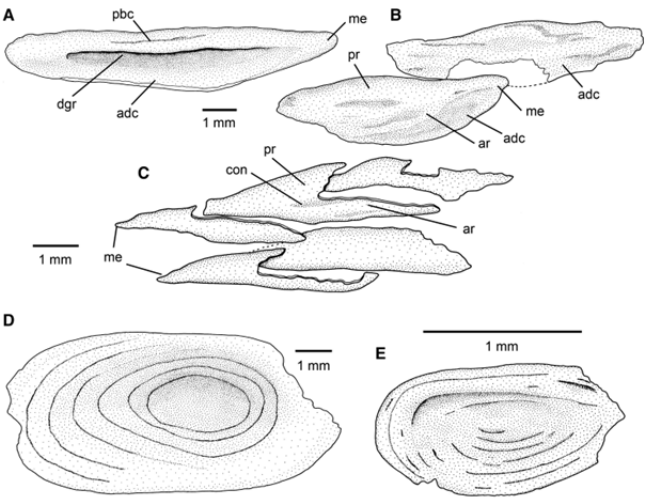

Fig. 3—**A–C.** MGUH 252. Scales of *Acanthostega gunnari*, (A) gastral scale in internal (dorsal) view, (B) gastral scales in external (ventral) view, (C) fragmentary articulating gastral scales in external (ventral) view. —**D–E.** PIN Collection 2921. Scales of *Tulerpeton curtum*, (D) gastral or dorsal scale in internal view (PIN 2921/3236), (E) Scale probably derived from the limbs in internal view (PIN 2921/3237).

rows or chevrons slightly overlap from anterior to posterior. Due to incomplete preservation, the morphology of the ventral midline of the gastral scalation cannot be determined. In contrast to colosteids, temnospondyls and 'anthracosaurs', posteriorly directed chevrons of the anterior part of the ventral trunk region are not visible, and thus nothing can be said concerning a possible 'nodal point' between anteriorly and posteriorly directed chevrons. Scales on the dorsal side of the body and the flanks are not preserved.

Ichthyostega sp. This second Famennian stem-tetrapod from East Greenland presents thin, rounded scales that overlap in an anterior to posterior direction and were described by Jarvik (1952) in the tail. However, these scales are too poorly preserved, so their morphology cannot be described in detail. Recently, J. A. Clack (in Daeschler *et al.* 2009) reported comma-shaped scales of *Ichthyostega* in cross-section, as characteristic for spindle-shaped gastral scales. Thus, it appears that *Ichthyostega* also possessed a similar gastral scalation as *Acanthostega* and many basal tetrapods.

Tulerpeton curtum. This stem-tetrapod from Famennian strata in Russia presents ovoid scales, probably covering the complete trunk (Fig. 3D), and smaller, more rounded scales in the limbs (Fig. 3E) (Lebedev and Coates 1995). These very thin scales possess concentric growth rings and show extensive anteroposterior overlap. The free external scale surface has short, longitudinal ridges. The overlapped surface possesses regularly arranged tubercles between the growth rings, whereas the internal scale surface is smooth. Both scales covering the trunk and the extremities are externally convex and internally concave, thus presenting the shape of a shallow bowl (personal observations), and resembling the ventrolateral scales of temnospondyls as *Archegosaurus* and *Sclerocephalus* (Witzmann 2007). An arrangement en-chevron of the ventral scales as for example in *Acanthostega* cannot be determined, possibly due to postmortem multiple folding of *Tulerpeton*'s skin (Lebedev and Coates 1995). However, the preserved rows of scales in *Tulerpeton* are arranged in a 'shallow S', which could indicate an indirect evidence of en-chevron arrangement of scales (personal observations).

Red Hill locality. Daeschler *et al.* (2009) reported stem-tetrapod remains from the late Famennian stage of Red Hill, Pennsylvania, USA. Among them, a gastral scale of an undetermined stem-tetrapod was found whose morphology corresponds to that of spindle-shaped gastral scales of temnospondyls and *Acanthostega*.

The scales in Early Carboniferous stem-tetrapods

Whatcheeriids. *Pederpes finneyae* is known from Tournaisian strata and constitutes the earliest known post-Devonian tetrapod with articulated postcranial skeleton (Clack and Finney 2005). Numerous moderately elongate, spindle-shaped gastral scales are preserved, resembling those of *Acanthostega*. In *Whatcheeria deltae*, recovered from strata of Viséan age, no gastral scales were reported (Lombard and Bolt 1995).

Crassigyrinus. The Viséan/Namurian *Crassigyrinus scoticus* from Scotland possesses spindle-shaped gastral scales, but no dorsal scales are preserved (Panchen 1985). As *Crassigyrinus* is a large-growing stem-tetrapod whose body length reached almost two metres, its gastral scales are quite large, measuring 30–40 mm in length.

Colosteids. These are early to middle Carboniferous stem-tetrapods (Ruta *et al.* 2003a), once thought to be either basal temnospondyls (Smithson 1982; Hook 1983) or representing the sister group of temnospondyls (Carroll 1995).

Greererpeton burkemorani. This taxon is known from upper Viséan/lower Namurian sediments of West Virginia. It is the best known colosteid (Smithson 1982; Godfrey 1989a,b). The gastral scales are well ossified and of rhombic outline (Fig. 4), closely resembling the gastral scales of the temnospondyls *Australerpeton* (Dias and Richter 2003), *Platyoposaurus* (Konzhukova 1955) and large adults of *Sclerocephalus* (Witzmann 2007). In contrast to the stem-tetrapods described above, posteriorly directed chevrons are visible in the anterior portion of the trunk, running parallel to the posterolateral margins of the interclavicle. They meet the anteriorly directed chevrons in a 'nodal point' as in temnospondyls, but without the 'undisturbed rows of scales' *sensu* Witzmann (2007) observed in many temnospondyls. In dorsal view, anterior margins of rhombic scales overlap posterior parts of the gastral scales from the preceding row dorsally, so that the chevrons overlap from anterior to posterior in ventral view (Fig. 4C). As in temnospondyls, the gastral scales in the posterior half of the trunk are thinner than those in the anterior half. Several gastral scales, especially the thicker ones in the anterior region, possess an irregular sculpture of ridges and knobs on their non-overlapped external surface (Fig. 4A). The gastral scales imbricate in a posterolateral direction within each row in the following way: each gastral scale bears a ventromedial facet that overlaps the dorsal surface of the neighbouring medial gastral scale from the same row. As described for the rhombic scales of temnospondyls (Witzmann 2007), this ventromedial facet is convex and bears a crest in its medial portion, whereas the lateral end of the facet has a concave surface. The dorsal or internal side of each rhombic gastral scale shows a distinct, dorsolaterally oriented facet or groove that measures about 70% of the length of the scale (Fig. 4B). The facet is anteriorly delimited by a sharp, deep crest that is directed anterodorsally, whereas it is posteriorly bordered by a lower, but thickened bulge-like crest. The lateral portion of the dorsolateral facet is plane to convex; it becomes increasingly concave medially and constitutes a conspicuous depression. The medial border of the facet is well defined and steep; medial to it, the dorsal surface of the scale is flat and becomes slightly

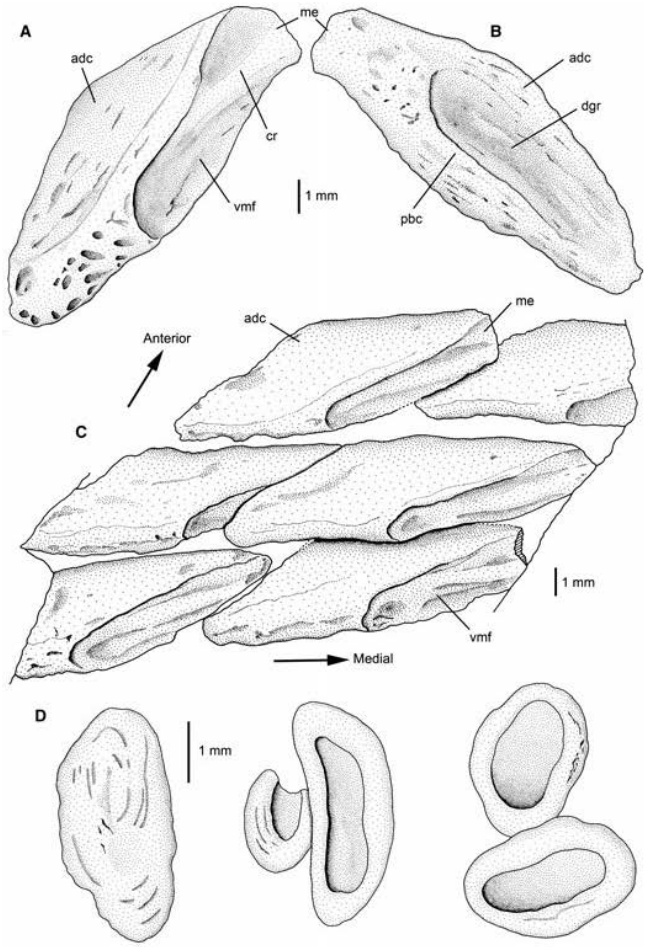

Fig. 4—Scales of *Greererpeton burkemorani*. —**A, B.** CMNH 11073. Gastral scale, (A) external (ventral) view, (B) internal (dorsal) view. —**C.** CMNH 11113. Articulating gastral scales in external (ventral) view. —**D.** CMNH 11113. Dorsal scales in external (left) and internal view.

convex at its medial end. The left and right rows of gastral scales articulate in the ventral midline as described for temnospondyls (Witzmann 2007; see also Claessens 2004), i.e. each medial-most gastral scale had a rounded medial end, the posterior portion of which is overlapped by the medial-most scale from the opposite row (see also Fig. 5D, E). Accordingly, the overlap in the ventral midline occurs alternating from left and right rows of scales. The flanks and the dorsal side of the trunk of *Greererpeton*, as well as its ventral pelvic region and the tail, are covered by scales that are circular to elongate oval (Godfrey 1989a; Witzmann 2007; Vickaryous and Sire 2009). These scales are designated here as 'round-oval scales' and are well ossified and bowl-shaped, i.e. externally convex and internally concave, and may show concentric growth rings (Fig. 4D). The scales show a regular overlap from anterior to posterior, forming a shingled roof.

Colosteus scutellatus . This colosteid from middle Pennsylvanian (Westphalian D) sediments of Linton, Ohio reached a smaller adult body size than *Greererpeton*. Several well-preserved postcranial remains with dorsal and ventral scalation are known (Hook 1983; personal observations). The ventral face of its trunk is covered by anteriorly directed chevrons of rhombic gastral scales, corresponding to the pattern found in *Greererpeton*. A 'nodal point' posterior to the interclavicle was also probably present. The non-overlapped external surface of

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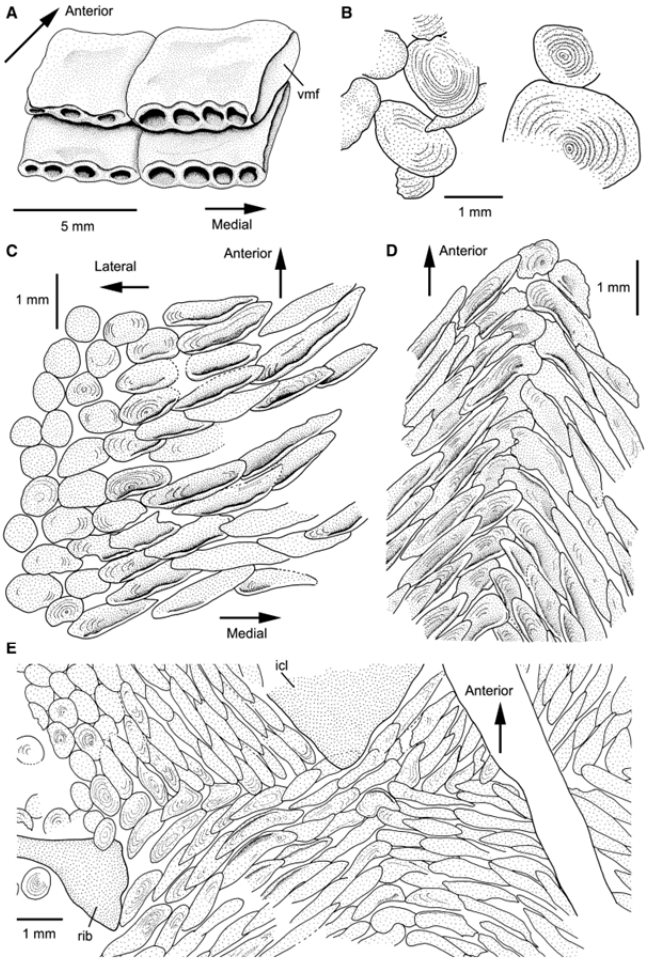

Fig. 5—A, B. AMNH 6917. Scales of *Colosteus scutellatus*, (A) rhombic dorsal scales in external view, (B) round dorsal scales in external view. —C–E. MB.Am.1203. Scales of larval *Sclerocephalus haeuseri*, (C) ventrolateral portion of gastral scalation in internal (dorsal) view, (D) ventral midline in internal (dorsal) view, (E) nodal point of anterolaterally and posterolaterally directed scale rows in internal (dorsal) view.

the gastral scales is sculptured by pits and tubercles, giving the posteroventral margin a serrated outline. The more lateral gastral scales are thinner, unsculptured and posses rounded corners (Hook 1983). The dorsal side of the trunk and the flanks are covered by similar rhombic scales (Fig. 5A) that are arranged in anteromedially directed rows. Thus, their pattern corresponds to that present on the ventral side. The dorsal rows show considerable anteroposterior overlap. Each rhombic dorsal scale has a slightly longer anteroposterior extension and is somewhat thinner than their rhombic counterparts from the ventral side (Hook 1983). The sculpture of the non-overlapped external surface is more regular than that of the gastral scales, consisting of a row of rounded-quadrangular cells delimited by narrow but rather deep ridges. The dorsal midline is poorly preserved and it is therefore not clear if the anteromedially directed rows of dorsal rhombic scales meet, forming complete anteriorly directed chevrons. The flanks between the dorsal and ventral rows of rhombic scales are covered by thin, round scales (Fig. 5B) that possess distinct concentric growth rings (see also Hook 1983). In the posterior part of the trunk, the rows of rhombic dorsal scales become shorter and are replaced by round scales (Hook 1983). These scales are also visible in the branchial region next to the gill bars (well visible in AMNH 6917). In addition to the round scales, subcircular, bony granules with a size up to 0.4 mm can be observed on the flanks between dorsal and gastral

rhombic scales (Hook 1983). Similar ossifications with a more irregular outline can also be found on the flanks of *Greererpeton* between gastral and round-oval dorsal scales (CMNH 11113).

Pholidogaster pisciformis. As demonstrated by Panchen (1975), *Pholidogaster* from Early Carboniferous rocks of Scotland is the third known genus of colosteids. Its postcranial skeleton was described by Huxley (1862) and Romer (1964). The ventral face of its trunk is covered by anteriorly directed chevrons of slender, spindle-shaped gastral scales.

Baphetids. This still enigmatic group of late Viséan to late Moscovian basal tetrapods was thought to represent basal temnospondyls (Beaumont 1977), but according to Ruta *et al.* (2003a), baphetids turned out to be stem-tetrapods more derived than colosteids. Milner and Lindsay (1998) described and illustrated gastral scales of *Baphetes* from Wigan that were probably arranged en-chevron. Each gastral scale has basically the morphology of the spindle-shaped scales of e.g. *Acanthostega* and temnospondyls. Milner *et al.* (2009) reported spindle-shaped gastral scales in *Baphetes orientalis* from Nýřany. The anterior portion of *B. orientalis* is preserved; interestingly, as Milner *et al.* (2009) recognized, it does not exhibit a nodal point as in colosteids, temnospondyls and 'anthracosaurs' (see below). Instead, its posteriorly directed rows do not change their orientation and meet the posterolateral margins of the interclavicle at a right angle. The very narrow, needle-like gastral scales of the small-growing *Eucritta melanolimnetes* (not a baphetid according to Ruta *et al.* 2003a) form anteriorly directed chevrons (Clack 2001). In the region of its pectoral girdle, no scales are preserved, thus the presence of a nodal point is uncertain. No dorsal scales are known in baphetids.

The scales in crown-group basal tetrapods

Temnospondyls. The morphology and arrangement of gastral and dorsal scales in temnospondyls was reviewed by Witzmann (2007). Temnospondyls are unique among basal tetrapods as they provide ontogenetic data of skeletal elements including the scales from small larvae to often large-growing adults. In early larval temnospondyls, the gastral scales are arranged en-chevron, but possess a round-oval morphology similar to that found in dorsal scales. During further ontogeny, the gastral scales attain a spindle-shaped (Fig. 5C, D) and eventually a rhombic morphology. Most adult temnospondyls retain the spindle-shaped morphology, which was interpreted as a paedomorphic trait (Witzmann 2007). A nodal point in which the anteriorly and posteriorly directed chevrons meet posterior to the interclavicle is present (Fig. 5E). The dorsal scales are thin, round and often show concentric growth rings and radial striae. A regular, anteroposterior overlap like in a shingled roof appears to be the plesiomorphic state for the dorsal scalation.

'Anthracosaurs'. This paraphyletic group of basal tetrapods encompasses embolomeres, eoherpetontids (postcranial material unknown), gephyrostegids and seymouriamorphs, and probably lies on the amniote stem (Ruta *et al.* 2003a). Among the earliest known 'anthracosaurs' are *Silvanerpeton mirripedes* and *Eldeceeon rolfi* from Viséan sediments of east Kirkton. *Silvanerpeton* has spindle-shaped gastral scales, and a nodal point is preserved posterior to the interclavicle (Clack 1994; fig. 2). *Eldeceeon* has slender, spindle-shaped gastral scales (Smithson 1994). In embolomeres, rhombic gastral scales arranged en-chevron were described for several taxa, but no dorsal scales were reported (Cope 1884; Panchen 1970; Holmes 1984; Clack 1987). However, Panchen (1970; fig. 17c) illustrated a block containing caudal vertebrae and scales of the embolomere *Nummulosaurus kolbi*. These scales are round and possess concentric growth rings. They apparently overlap anteroposteriorly and closely resemble the dorsal scales of many temnospondyls. In gephyrostegids, spindle-shaped to rhombic gastral scales that are arranged en-chevron are present, and gastral scales become more circular on the lateral side of the ventral trunk region (Carroll 1972). In *Gephyrostegus bohemicus*, the spindle-shaped gastral scales may possess growth rings and have a groove posterior and parallel to the posterior bulge-like crest in dorsal view (Fig. 6A). In the ventral midline, the medialmost gastral scales have slightly broadened medial ends. A nodal point of spindle-shaped gastral scales was present, as indicated by anterolaterally directed rows of scales posterior to the interclavicle (Fig. 6B). In MB.Am.1901.1378, numerous thin, round scales are visible dorsal to the vertebral column. They possess concentric growth rings and fine radial striae, thus closely resembling the round-oval scales of temnospondyls and *Colosteus*. The enigmatic *Solenodonsaurus janenschi*, which might be a stem-amniote (Laurin and Reisz 1999; Ruta *et al.* 2003a) or a crown amniote (Ruta *et al.* 2003b), has spindle-shaped gastral scales and round dorsal scales with growth rings (Carroll 1972). Among seymouriamorphs, 'discosauriscids' have bodies that are completely covered by overlapping, round to ovoid scales that bear numerous growth rings (Špinar 1952; Ivakhnenko 1987; Bulanov 2003). Klembara and Bartík (2000) reported concentric growth rings that are intersected by radial striae, resulting in a net of individual fields on the external scale surface. In most 'discosauriscids', the scales are oriented in transverse and longitudinal rows. Ivakhnenko (1987; fig. 2) and Klembara and Ruta (2004; fig. 7b) reported ovoid gastral scales with growth rings in *Utegenia shpinari*, which are internally concave and have a posteriorly thickened margin. This corresponds to early juvenile gastral scales of temnospondyls *sensu* Witzmann (2007). The gastral scales in *Utegenia* are arranged en-chevron, with a nodal point posterior to the interclavicle (Klembara and Ruta 2004; fig. 2a). Laurin (1996) found round dorsal scales in the same taxon. In other 'discosauriscids', as *Ariekanerpeton* and *Discosauriscus*, the scales were described or illustrated in transverse and longitudinal rows (e.g. Ivakhnenko 1987; Klembara and Bartík 2000).

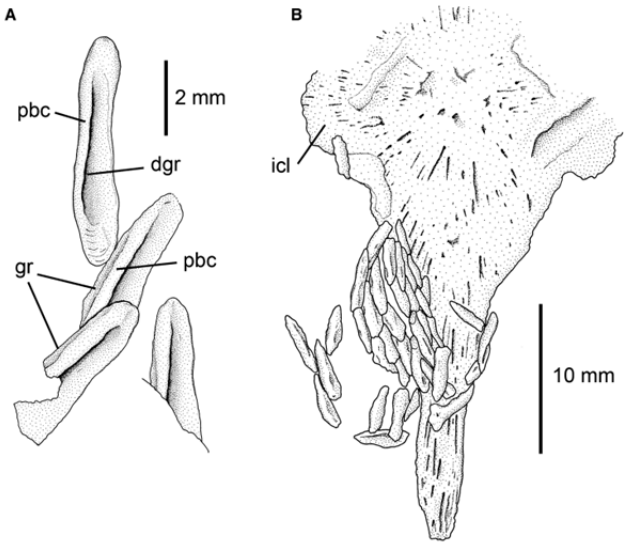

Fig. 6—Scales of *Gephyrostegus bohemicus*. —**A.** MB.Am.719a. Gastral scales in internal (dorsal) view. —**B.** MB.Am.719b. Interclavicle with anterolaterally directed rows of gastral scales in external (ventral) view, indicating the presence of a nodal point.

Lepospondyls . Lepospondyls are a diverse group of Palaeozoic basal tetrapods, which are probably closely related to amniotes (Laurin and Reisz 1997; Ruta *et al.* 2003a). According to Ruta *et al.* (2003a), lepospondyls are more closely related to amniotes than to lissamphibians. Anderson *et al.* (2008) regarded caecilians as derived from lepospondyls, whereas Laurin and Reisz (1997) and Vallin and Laurin (2004) held the view that all lissamphibians are lepospondyls. In microsaurs, the trunk, the tail and the limbs are completely covered by extensively overlapping scales (Carroll 1998a). Their gastral scales are often more elongate and thicker than the dorsal ones, and are arranged in a chevron pattern. Ventrolaterally, a gradual transition of the gastral scales into the rounded-oval scales of the flanks and the dorsal side of the trunk is visible. Some microsaur taxa have scales bearing an ornamentation of ridges and striae that closely resembles the scales of micromelerpetontid temnospondyls (Fritsch 1883; Boy and Sues 2000). Acherontiscids have scales similar to those of microsaurs (Carroll 1998b).

Most 'nectrideans' have spindle-shaped gastral scales arranged en-chevron (Bossy and Milner 1998). Their length varies among taxa, and the external surface may be sculptured or not. Rounded dorsal scales have been demonstrated only in *Keraterpeton longtoni* (Bossy and Milner 1998). In adelospondyls, the ventral face of the trunk is covered by spindle-shaped gastral scales, whereas the dorsal scales are rounded-oval, very thin and bear fine concentric rings and radial ridges (Carroll and Andrews 1998). The spindle-shaped gastral scales arranged en-chevron of aïstopods are quite narrow and elongate, so that they can be designated as needle-like (Carroll 1998c; Anderson 2003). On the dorsal side of the body, diamond-shaped or rounded dermal ossifications are present.

Histology of dermal scales in Panderichthys rhombolepis, colosteids and temnospondyls

Panderichthys . As described by Gross (1930), the scales of *Panderichthys* do not bear dentine and enamel components, so the dermal sculpture of tubercles and ridges is solely composed of bone. In vertical section, the following layers can be distinguished (Fig. 7A): (1) a thick, sculptured external compact layer; (2) a rather thin, well vascularised middle layer; (3) a thick basal layer consisting of isopedine; (4) internal bone tissue that constitutes the internal keel of the scale. The tubercles and ridges of the external layer appear as saddles in the sections, and the bone surface between them as valleys. The bone matrix of the external layer consists of fine parallel-fibred bone with a large number of bone cell-lacunae. In the saddles, the lacunae are mostly rounded, whereas in the valleys, they are often spindular and arranged parallel to their longitudinal axes. Similar to odontode-bearing bone (Bystrow 1939), tubercles of earlier generations that were 'buried' by the appositional growth of the bone are visible in the external layer. Growth marks are clearly detectable. The external layer is moderately vascularised with primary vascular canals that may anastomose (Fig. 7B). Scattered secondary osteons are also discernable. Fine, fan-shaped Sharpey's fibres that are mineralised penetrate the saddles, whereas only a few fibres are visible in the valleys. No resorptive structures are visible at the bone surface, so the dermal sculpture developed solely by

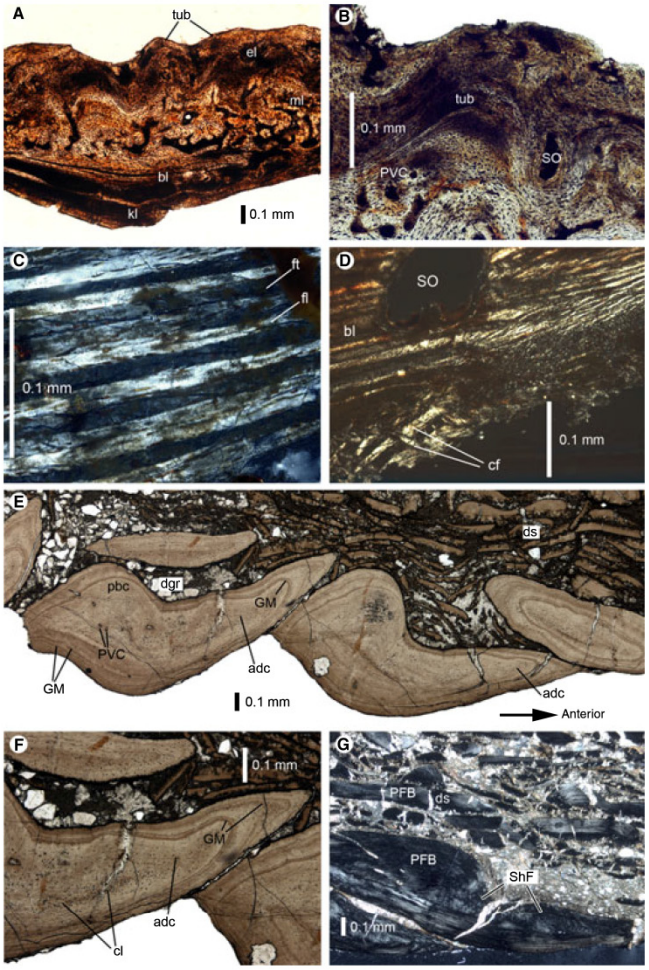

Fig. 7—A–D. *Panderichthys rhombolepis*. Histological thin sections of scales, (A) MB.Hi.415. Transverse section, overview, (B) MB.Hi.415. Close up of external and middle layer, (C) MB.f.1891.3. Basal layer consisting of isopedine. Polarized light, (D) MB.Hi.413. Basal layer and parts of the keel, which is penetrated by strong connecting fibres. Polarized light. —E–G. CMNH 11113. Histological sections of gastral and dorsal scales of *Greererpeton burkemorani*, (E) articulating gastral scales in transverse section. The gastral scales are overlain by numerous fragmentary dorsal scales, (F) close up of the anterodorsally directed crest of a gastral scale, (G) gastral scale in longitudinal section with overlying fragmentary dorsal scales. The bone matrix of both scale types consists of parallel-fibred bone. Polarized light.

preferential bone growth as in sculptured dermal skull bones (Bystrow 1935; Castanet *et al.* 2003; Witzmann and Soler-Gijón 2010). The middle layer is quite thin and well vascularised, thus appearing coarse cancellous. The primary matrix consists mostly of fine parallel-fibered bone. Secondary osteons are present, but they are not numerous. The middle region is separated from the thick basal layer by a distinct transition. This basal layer exhibits a plywood-like structure that can be designated as isopedine (Fig. 7C). In polarized light, a regular pattern of horizontal bands is visible. Those bands in which the fibres are cut longitudinally appear bright or dark under polarized light (with elongate cell-lacunae), whereas those in which the fibres and bone cell-lacunae are obliquely cut brighten up to a lesser extent. Bands with transversely cut fibres remain dark in polarized light (with round cell-lacunae). Vascularisation is scarce; scattered primary vascular canals and few secondary osteons run parallel or oblique to the internal scale surface. As already mentioned by Gross (1930), the bony tissue of the keel is visible internal to the basal layer of isopedine (Fig. 7A, D). Under polarized light, it is well visible that thick, mineralised fibres penetrate the keel obliquely from anterior and posterior and meet each other at about 90° (Fig. 7D). Kerr (1952) and Gemballa and Bartsch (2002) described similar fibres in the keel of the rhombic scales in

Polypterus. However, in the latter the fibres do not intersect. The fibres penetrating the keel of *Polypterus* connect the scale rows to each other, and a corresponding function of the fibres can be assumed for those penetrating the keel of *Panderichthys*.

Greererpeton . The histology of both the ventral and dorsal scales of *Greererpeton* was investigated for this study. The gastral scales show the typical 'comma shape' in cross-section, with the dorsal groove delimited by the posterior bulge and the anterodorsal sharp crest (Fig. 7E, F). The bone tissue of the scales is composed throughout of parallel-fibred bone (Fig. 7G). Vascularisation is sparse and consists of scattered primary vascular canals. Secondary osteons cannot be observed. The scales are compact and do not possess a marrow cavity or cancellous region. Rounded to ovoid bone cells are frequently visible, but they are by far not as abundant as in the scales of *Panderichthys*. Circumferential growth marks are distinct. They show a positive allometric growth of the anterodorsal crest (Fig. 7F). In polarized light, thin Sharpey's fibres are observable that penetrate the scale circumferentially. In the ventromedial facet, the Sharpey's fibres are thick and densely arranged, connecting the scales within a row (Fig. 7G). Corresponding to the gastral scales, the dorsal scales consist solely of parallel-fibred bone (Fig. 7G). They are distinctly thinner than the gastral scales. Ovoid bone cells are present, but less abundant than in the gastral scales. Growth marks are distinct and show a concentric pattern. The dorsal scales are practically avascular and no secondary remodelling is present (Fig. 8A). Interestingly, no Sharpey's fibres can be detected in these scales.

Temnospondyls . Histological investigations of temnospondyl gastral scales have so far been restricted to the basal stereospondyl *Australerpeton* (Dias and Richter 2003). Bone histology closely resembles that described above for *Greererpeton*. The scales consist solely of bone tissue and show circumferential growth marks. Sharpey's fibres that penetrate the bone indicate that the scales were imbedded within the dermis. In juvenile specimens, the scales are compact, whereas the scales of adults have a cancellous core with secondary osteons, showing that remodelling with resorption and redeposition of bone took place (Dias and Richter 2003). In the present contribution, the gastral scales of the plagiosaurids *Plagiosuchus*

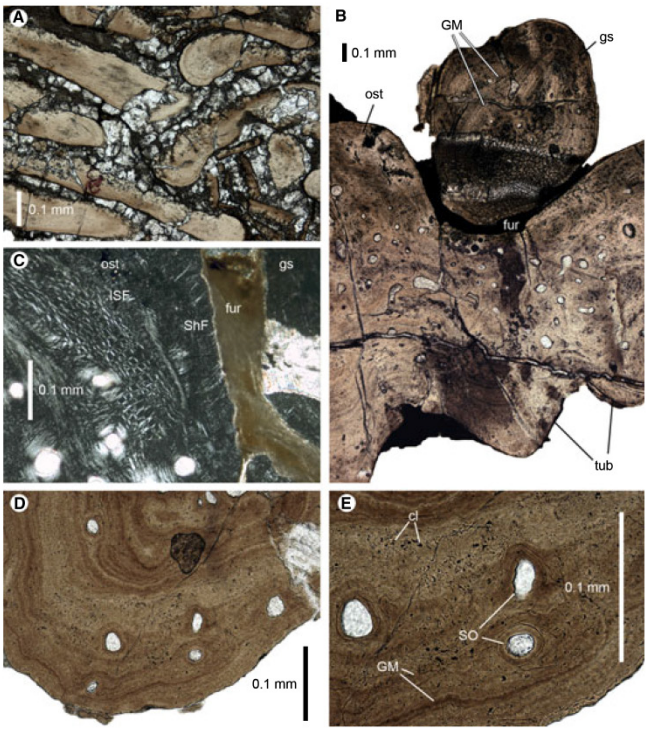

Fig. 8—**A.** CMNH 11113. Histological sections of dorsal scales of *Greererpeton burkemorani*. —**B, C.** SMNS 91342. Histological sections of gastral scale plus osteoderm of *Gerrothorax* sp., (B) Gastral scale in transverse section, located in a furrow on the underlying ventral osteoderm, (C) Close up of the furrow between the dorsal surface of the osteoderm and the gastral scale; Sharpey's fibres are visible that connected the two elements in the living animal. The bone matrix of the gastral scale consists of parallel-fibred bone, and the osteoderm consists of parallel-fibred bone and interwoven structural fibres. —**D, E.** SMNS 84794. Histological section of gastral scales of *Plagiosuchus pustuliferus*, showing growth marks and small secondary osteons.

pustuliferus and *Gerrothorax* sp. from the Middle Triassic of southern Germany have been investigated histologically. *Gerrothorax* (Nilsson 1946; Hellrung 2003; Witzmann 2007) has slender, elongate gastral scales that are located in furrows on the dorsal side of the plate-like ventral osteoderms. Their anteromedially directed rows (forming the chevron pattern) are reduced in number and well separated from each other in comparison to most other temnospondyls (Witzmann 2007). Thin section reveals that the gastral scales consist of compact, cellular bone (Fig. 8B). Spindular bone cell-lacunae are numerous, and canaliculi are not visible, possibly an artefact of preservation. Circumferential growth marks are clearly visible in transverse section. Vascularization is poor to moderate and consists mainly of primary vascular canals that are often oriented in parallel to the longitudinal axis of the gastral scales. Only very few, isolated secondary osteons of small diameter are present. The primary bone matrix consists of parallel-fibred bone, and rather thin Sharpey's fibres are visible in polarized light. On the dorsal side of the underlying ventral osteoderm, the furrow that accommodates the gastral scale is well visible (Fig. 8B). In polarized light, Sharpey's fibres are visible in the margins of the furrow, connecting the osteoderm and the gastral scale in the living animal (Fig. 8C). The osteoderm consists mainly of parallel-fibered bone with growth marks, and scattered areas of interwoven structural fibres are present (Fig. 8C). The gastral scales of *Plagiosuchus* correspond in morphology, arrangement and histology (Fig. 8D, E) to those of *Gerrothorax*, but no plate-like osteoderms are present ventral to them. Instead, tiny mineralised nodules occur ventral to the gastral scales (Witzmann and Soler-Gijón 2010).

Discussion

Ancestral osteichthyan scales and their arrangement

Schultze (1977) reconstructed the hypothetical ancestral scale of stem-osteichthyans as being thick and rhombic in outline, with dentine tubercles (not capped by enamel or enameloid) covering a cancellous layer of bone, which is followed internally by a basal layer of lamellar, plywood-like bone tissue (i.e. isopedine). Each scale possessed a distinct keel on its internal surface. These scales were arranged in oblique rows on the body in basal osteichthyans, and each scale was overlapped by adjoining scales anteriorly and dorsally on the external surface and ventral to the keel on the internal side (Schultze 1977). Sire *et al.* (2009) additionally hypothesized the presence of elasmodine (a plywood-like dentinous tissue) in the ancestral rhombic scale and thus also in the rhombic ganoid scales of actinopterygians and the rhombic cosmoid scales of sarcopterygians. The cosmoid scale was originally characterized by cosmine, a sheet-like orthodentine capped by enamel/enameloid housing a pore canal system (Gross 1966; Janvier 1996; Sire *et al.* 2009). Internal to the cosmine, the cosmoid scale was possibly composed of elasmodine (Sire *et al.* 2009), vascular bone and a basal layer of isopedine (Gross 1966). In dipnomorph fishes and in the tetrapod stem-group, the dental components were increasingly reduced and several lineages like dipnoans, holoptychiids and tristichopterids evolved rounded scales. The scales of 'elpistostegids' are derived in the absence of cosmine and the presence of dermal sculpture that is composed solely of bone, but are plesiomorphic in their rhombic outline and arrangement in oblique rows. Among 'elpistostegids', the scales of *Elpistostege* resemble most closely those of tetrapods in their increased length (more elongate in shape) and in their vermiculate dermal sculpture. As shown above, *Panderichthys* has anteromedially directed rows of rhombic scales both on the ventral and the dorsal face of the body, meeting on the ventrolateral side of the trunk in the 'ventrolateral ridge'. This pattern can be assumed for all 'elpistostegids' and is probably plesiomorphic for 'osteolepiforms', as it can also be observed in osteolepids (Jarvik 1948; personal observations). It is unclear, however, if this pattern was already present in stem-osteichthyans, or if the latter possessed rows of scales that were arranged in an anterodorsal to posteroventral direction, as seen in the majority of basal actinopterygians (Schultze 1966; Gemballa and Bartsch 2002). However, Jessen (1972) reported an arrangement of rhombic scales in the Devonian basal actinopterygian *Moythomasia nitida* that corresponds closely to that described above in *Panderichthys*, with a row of median dorsal and ventral scales, anteromedially directed dorsal and ventral rows of rhombic scales, and a 'ventrolateral ridge' of 'inversion scales'. 'Elpistostegids' are most closely related to limbed tetrapodomorphs (Vorobyeva and Schultze 1991; Ruta *et al.* 2003a; Shubin *et al.* 2006), and the rhombic morphology of the scales, their arrangement and the mode of overlap closely resemble the gastral scales of limbed tetrapodomorphs. Therefore, the gastral scales of limbed tetrapodomorphs can directly be compared with – and must be derived from – those of 'elpistostegids'.

Development of scalation in limbed tetrapodomorphs

Alteration of the arrangement of ventral scales. Although the gastral scales of stem-tetrapods and basal tetrapods show an arrangement that corresponds to the ventral scale rows of 'elpistostegids' and many 'osteolepiforms', they possess no median row of scales. Instead, the medialmost gastral scales from opposite sides show alternating overlap (see above; Fig. 5D). Interestingly, Jarvik (1948) reported paired median dorsal scales in some osteolepid specimens and thus suggested that at least the median dorsal scale row is of paired origin. This could also apply for the ventral row. Therefore, the median row of scales was either completely reduced in stem-tetrapods, or they might have returned to the ancestral state of paired median scales. However, the morphology of the ventral midline is not preserved in any Devonian stem-tetrapod, so it cannot be stated if a median row of scales was present or not. Characteristic for many basal tetrapods is the 'nodal point' in

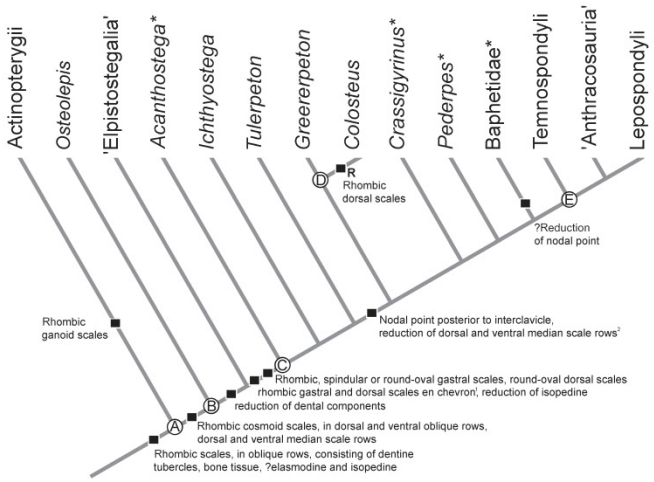

Fig. 9—Scale morphology and arrangement in finned and limbed sarcopterygians as well as actinopterygians, mapped on an existing cladogram based on the results of Ruta *et al.* 2003a and Coates *et al.* 2008. *Taxa in which no dorsal scales are preserved. [1]Although rhombic gastral and dorsal scales have not been observed in known Devonian limbed tetrapodomorphs (in contrast to spindle-shaped and round-oval scales) their presence as a basal character of limbed tetrapodomorphs is hypothesized here, based on comparison with finned tetrapodomorphs and the colosteid *Colosteus*. [2]These two characters appear at the latest in colosteids crownwards but might have appeared earlier in limbed tetrapodomorphs; incomplete preservation of fossils precludes a definite statement. For further explanations see text. Abbreviations: A, Osteichthyes; B, Sarcopterygii; C, limbed tetrapodomorphs; D, Colosteidae; E, crown-group Tetrapoda; R, reversal.

the anteroventral region of the trunk, in which the anteriorly and posteriorly directed chevrons of gastral scales meet (Fig. 5E) (Witzmann 2007). In 'osteolepiforms' and 'elpistostegids', all ventral oblique rows of scales are posterolaterally directed and no 'nodal point' is present. Unfortunately, this region is not preserved in Devonian stem-tetrapods, and a 'nodal point' seems to be absent in baphetids, as the rows of gastral scales do not change their orientation lateral to the interclavicle (Milner *et al.* 2009). Comparison with finned sarcopterygians suggests that this could represent the plesiomorphic state. The basal most stem-tetrapods in which a 'nodal point' is visible are colosteids; it is further present in temnospondyls and the amniote lineage (see above). The development of morphology and arrangement of dermal scales in finned and limbed tetrapodomorphs is summarized in Fig. 9.

Origin of the rhombic gastral scale . To understand how scale morphology was altered during the fish-tetrapod transition, it is necessary to identify homologies in the rhombic scales of 'elpistostegids' and the gastral scales of limbed tetrapodomorphs (Fig. 10A–C). 'Landmarks' in the 'elpistostegid' scale are first the keel on the internal surface, which serves as anchoring point for Sharpey's fibres to connect the different oblique rows of scales in osteichthyans (Kerr 1952; Schultze 1966; Gemballa and Bartsch 2002; this study), and which frames the internal facet of the scale. Second are the articulation facets and the (sculptured) free external surface. The morphological transformation between the 'elpistostegid' scale and the gastral scale of limbed tetrapodomorphs can be reconstructed as follows. The internal articulation facet became proportionally distinctly longer, measuring more than half the length of the scale. The keel became correspondingly shorter, but increased in width and occupied the width of the medial portion of the scale. It still frames the internal articulation facet (or dorsal groove), but over a longer distance than in the 'elpistostegid' scale. Posteriorly, the frame is formed by a thickened, deep bulge, and anteriorly by a more slender, anterodorsally oriented crest. In this way, the internal facet became conspicuously deeper in limbed tetrapodomorphs and can now be designated as 'dorsal groove'. The area on the external surface that was overlapped by the anterior scale row proportionally increased in size. Accordingly, the free surface of the scale became narrowed. The external facet of articulation attained an elaborate, concavo-convex surface. These morphological alterations caused (1) a tighter connection between the gastral scales within a scale row, and (2) increased anteroposterior overlap between the scale rows (see below).

Histologically, the gastral scales of limbed tetrapodomorphs show a simplification when compared with the rhombic scales of 'elpistostegids'. The gastral scales investigated in this study consist uniformly of parallel-fibred bone that bears

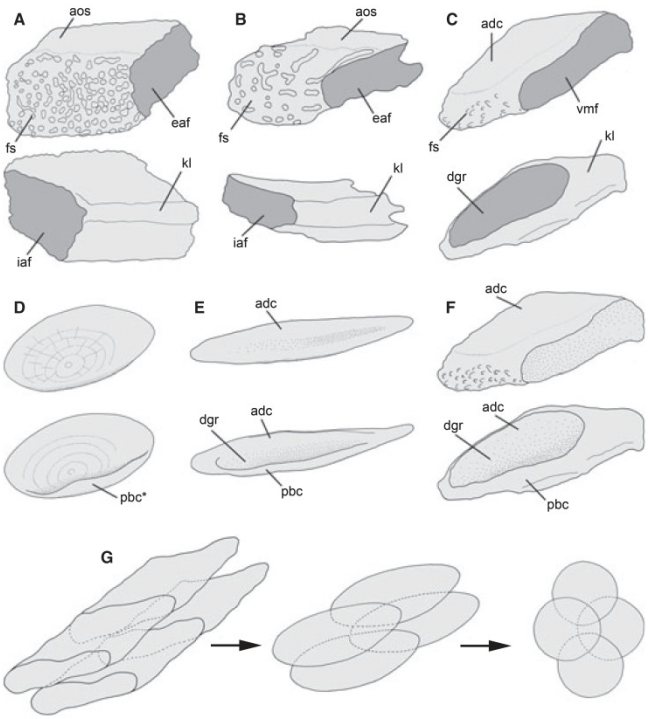

Fig. 10—**A–C**. Comparison of 'elpistostegid' scales and limbed tetrapodomorph gastral scales in external view (top) and internal view (bottom), schematic drawings, not to scale, (A) *Panderichthys rhombolepis*, (B) *Elpistostege watsoni*, redrawn from Schultze and Arsenault 1985, (C) *Greererpeton burkemorani*. —**D–F**. Comparison of round, spindle-shaped and rhombic gastral scales in external view (top) and internal view (bottom), schematic drawings, not to scale, (D) larval *Sclerocephalus haeuseri*, (E) late larval *Archegosaurus decheni*, (F) adult *Greererpeton burkemorani*. —**G.** Arrangement of rounded dorsal scales in limbed tetrapodomorphs (right), and its probable derivation from the oblique rows of rhombic scales. Schematic drawing, anterior is left.

circumferential growth marks. The thick basal layer consisting of isopedine (lamellar bone) is completely reduced. Corresponding histological results were reported from gastral scales of the basal stereospondyl *Australerpeton* (Dias and Richter 2003).

Scale ontogeny: rounded and spindle-shaped gastral scales . Schoch (2003) and Witzmann (2007) reported thin, ovoid gastral scales with concentric growth rings in early growth-stages of temnospondyls, closely resembling their dorsal scales (Fig. 10D). This gastral scale morphology was designated as 'larval' by Witzmann (2007). In ontogenetically more advanced temnospondyl larvae, the development of the posterior bulge and the proportional elongation of the scale and thus the transition to the spindle-shaped morphology can be followed. The presence of ovoid gastral scales in adult specimens, e.g. in *Tulerpeton*, can thus be interpreted as a retained 'larval' or early ontogenetic morphology. Spindle-shaped gastral scales, as seen for example in *Acanthostega* or in the Devonian stem-tetrapod from Red Hill, and rhombic gastral scales can be traced back to basically the same morphology (Fig. 10E, F). Compared with the rhombic scale, the spindle-shaped scale is proportionally elongate and slender, with a more tapering medial end. Accordingly, the dorsal groove is relatively longer. As in the rhombic scale, the dorsal groove is framed posteriorly by a bulge-like crest and anteriorly by a more slender crest, which is, however, much lower than in the rhombic gastral scale. Due to the small size of the anterior crest, there is no (or little) overlap between the rows of spindle-shaped scales. Rather, the anterior margin of each spindle-shaped gastral scale abuts against the thickened posterior margin of the adjacent gastral scale of the preceding row.

As described by Witzmann (2007), the spindle-shaped gastral scales can be regarded as the ontogenetic precursor of the rhombic gastral scales in several temnospondyls (well visible especially in *Sclerocephalus*). The rhombic outline is attained by the expansion of the slender crest that borders the dorsal groove anteriorly, and by a thickening of the posterior bulge-like crest. The anterior crest underwent accelerated growth in an anterodorsal direction and became deeper than the posterior crest. The expanded anterior crest overlaps the internal surface of the adjoining scales of the anterior row, thus forming the anterior overlap surface of the gastral scale described above (Fig. 4C). The largely smooth dorsal groove of the spindle-shaped gastral scales becomes the well-defined facet

or groove of the rhombic gastral scale, with a slightly convex lateral portion and a concave medial portion (see above). The slightly concave area between the anterior and posterior ridge on the ventromedial surface of the spindle-shaped scales (see description of *Acanthostega* above; Figs. 3C, 10E) differentiates into the well-defined ventromedial facet of the rhombic gastral scale (Witzmann 2007).

As the morphology of both spindle-shaped and rhombic gastral scales in stem-tetrapods corresponds closely to that seen in temnospondyls, it can be assumed that they basically shared the same ontogenetic pattern. This view is supported by the histological sections of the rhombic gastral scales of *Greererpeton*, in which the growth marks indicate a positive allometric growth of the slender anterodorsal crest (Fig. 7E, F).

Dorsal scalation . Although a rounded dorsal scale has no similarity with a rhombic 'elpistostegid' scale at first sight, it is more parsimonious to assume that they were derived from the 'elpistostegid'-type of scale rather than being *de novo* structures. Similar examples can be seen in the evolution of actinopterygians and fish-like sarcopterygians, in which the rhombic ganoid and cosmoid scales, respectively, were independently modified several times into thinner, rounded scales (Gross 1966; Schultze 1966, 1977; Janvier 1996; Sire *et al.* 2009). Morphological transformation from rhombic to rounded dorsal scale during the fish-to-tetrapod transition might have happened as follows. In the 'larval' ovoid scale, proportional elongation of the scale ceased early in ontogeny, and so did the development of the posterior crest. Further growth of the scale was more compensational, resulting in a rounded shape. Early in tetrapod evolution, the dorsal scales might have been more intermediate in morphology, similar to the dorsal scales in *Greererpeton*. These scales are still well ossified and strongly concave internally (ventrally), but they have rounded edges and are bilaterally symmetrical. This evolutionary scenario is reflected in the lateral parts of the gastral scalation in limbed tetrapodomorphs and basal tetrapods: the more laterally located spindle-shaped or rhombic gastral scales become increasingly thinner, show concentric growth rings and rounded edges, and their shape becomes more symmetrical (Fig. 5C). Thus, there is almost a continuous transition visible from gastral scale to round dorsal scale morphology. A comparable situation can be observed in certain fossil basal actinopterygians, which have rhombic and round scales, and all transitional morphological stages between them are present in the same individual (Schultze 1966). As gastral and dorsal scales probably develop from the same *anlagen*, round-ovoid 'dorsal' scales can also be observed to cover the ventral face of the trunk, as in *Tulerpeton* (Lebedev and Coates 1995), trimerorhachids (Colbert 1955; Chase 1965; Berman 1973; Witzmann 2007), branchiosaurids (e.g. Boy and Sues 2000), 'microsaurs' (e.g. Carroll 1998a) and 'discosauriscids' (e.g. Klembara and Bartik 2000). The situation in *Colosteus* strongly supports the assumption that dorsal scales in limbed tetrapodomorphs are derived from dorsal rhombic scales and posses the same *anlage* as gastral scales. As described above, the dorsal scale morphology of *Colosteus* is the same as that of rhombic gastral scales. They are correspondingly arranged in posterolaterally directed rows. This development can be interpreted as a reversal, showing that the dorsal scale *anlagen* still have the ability to retain the plesiomorphic rhombic scale morphology. In limbed tetrapodomorphs, round dorsal scales were probably plesiomorphically overlapping and oriented in transverse rows, as visible in *Ichthyostega* and *Greererpeton*. The anterior portion of each dorsal scale is overlapped by three scales: two from anterodorsal and anteroventral, respectively, and one scale that overlaps all three scales from anterior. This pattern can easily be derived from oblique rows of rhombic scales (Fig. 10G). A similar pattern was assumed by Jarvik (1980) for rhombic and round scales of osteolepids and rhizodontids. As described by Witzmann (2007), several derived temnospondyls have non-overlapping dorsal scales which have often no point of contact at all. Regarding scale development in actinopterygians (Schultze 1966; Sire and Akimenko 2004), this might be interpreted as paedomorphic and represents the apomorphic state. Embolomeres, gephyrostegids, 'discosauriscids' and 'microsaurs' show the plesiomorphic overlap of dorsal scales.

If the interpretation that the round dorsal scales of limbed tetrapodomorphs are derived from the dorsal oblique rows of 'elpistostegid'-type scales is correct, then the boundary between gastral and dorsal scales represents the old 'ventrolateral ridge', where the dorsal and ventral oblique rows of 'elpistostegids' and many 'osteolepiforms' meet at an angle. Jarvik (1948) suggested that this ridge probably indicates the ancient paired ventrolateral fin fold.

Evolutionary and functional implications

Devonian limbed tetrapodomorphs already possess the derived scale morphology of gastral and round-oval scales. This morphology was retained in basal tetrapods and became a very conservative character, affecting both the temnospondyl (amphibian) and the amniote lineage. Spindle-shaped gastral scales arranged en-chevron were maintained also in early amniotes (Carroll and Baird 1972) and even in basal diapsids (Bickelmann *et al.* 2009). In contrast, although 'elpistostegids' show conspicuous tetrapod-like characters in their skull, pectoral girdle, limbs and ribs (Schultze and Arsenault 1985; Vorobyeva and Schultze 1991; Daeschler *et al.* 2006; Shubin *et al.* 2006; Downs *et al.* 2008), their scale morphology and arrangement represents the plesiomorphic pattern similar to that found in osteolepids (Jarvik 1948), with the exception that all dental components are reduced. Thus, the morphological and histological transformation between the 'elpistostegid' type of scale in finned tetrapodomorphs and the gastral and dorsal scales of limbed tetrapodomorphs must have occurred very rapidly, probably contemporaneously with the origin of digitized limbs. This raises the question of a possible

functional correlation between the presence of limbs and the alteration of the scalation. The transformation of the scalation pattern might have been connected with the need for a more flexible trunk during terrestrial or semiterrestrial locomotion, and a reduction of weight. The following characters indicate that the gastral and dorsal scalation in limbed tetrapodomorphs was more flexible and probably allowed a larger degree of trunk flexion of the trunk compared with 'elpistostegids': (a) the ventral median row of scales that firmly interconnects the scale rows of both lateral sides of the body is reduced, instead, the contralateral rows of scales articulate in an alternating, overlapping fashion; (b) the mode of overlap of the spindle-shaped ('juvenile') gastral scales allowed telescoping of the scales within the rows during sideward flexion of the body; (c) although the rhombic ('adult') gastral scales were more tightly connected within the rows, the anterior overlap surface became proportionally larger than in 'elpistostegids', allowing more overlap between scale rows; (d) dorsal scales were thinner and certainly more flexible than ancestral rhombic scales. Additionally, the evolution of a 'nodal point' in gastral scalation is present from colosteids crownwards and might have facilitated sideward movements of the head plus pectoral girdle: when head plus girdle moved to one lateral side, the degree of overlap between the anterolaterally directed rows of this side increased, whereas the degree of overlap between rows of the other side decreased. As the forelimbs are located lateral to the nodal point in the 'gap' between anterolaterally and posterolaterally directed rows, the nodal point might have provided a greater degree of freedom to the forelimbs.

Compared with their finned ancestors, the histological scale structure in limbed tetrapodomorphs is simplified, resulting in a physiologically less expensive development of dermal scales: in both dorsal and ventral scales of limbed tetrapodomorphs, the thick basal layer of isopedine was reduced, and the transformation of thick dorsal rhombic scales into much thinner rounded-oval scales led to a reduction in weight of the animal and might also have enabled cutaneous respiration to a certain degree.

Conclusions

1. One of the most rapid morphological changes during the fish-to-tetrapod transition in the Devonian affected the skin. Apparently at roughly the same time when digits appeared, the rhombic scales of finned tetrapodomorphs were altered and differentiated into ventral gastral and dorsal round scales. Once established in limbed tetrapodomorphs, especially the gastral scales were retained as a conservative character in different lineages of basal tetrapods, in both amphibian and amniote lineages.
2. Gastral scales are derived from the 'elpistostegid'-type scale by an enlargement and differentiation of the internal and external articulation facets, shortening and broadening of the keel, and a proportional enlargement of the anterior overlap surface. These morphological changes caused a tighter connection between the gastral scales within a scale row and a greater anteroposterior overlap between the scale rows.
3. 'Elpistostegids' (and several 'osteolepiforms') have posterolaterally directed rows of rhombic scales on the ventral and on the dorsal side of the trunk. These rows meet on the ventrolateral side of the trunk in the so called 'ventrolateral ridge', which might represent the boundary between gastral and dorsal scales in limbed tetrapodomorphs. The posterolateral direction of scale rows was retained in the gastral scalation of most limbed tetrapodomorphs and basal tetrapods, whereas the arrangement of the round dorsal scales is modified to a transverse orientation in most taxa.
4. The gastral and dorsal scales can be traced back to the same *anlagen*. The dorsal round scale developed from a gastral scale-type by an alteration of the ontogenetic pathway.
5. Spindle-shaped and rhombic gastral scales possess basically the same morphology. The spindle-shaped scale is the ontogenetic precursor of the rhombic scale at least in some temnospondyls. The variation of gastral scale morphology in different limbed tetrapodomorphs and basal tetrapods is caused, on the one hand, by ontogenetic truncation of development in several taxa, and by different allometric growth of parts of the scale on the other hand.
6. Both gastral and dorsal scales of limbed tetrapodomorphs show a simplification of their histology compared with the scales of 'elpistostegids'. They uniformly consist of parallel-fibred bone with circumferential growth marks, and the thick basal layer of isopedine is completely reduced. In contrast to osteoderms of several temnospondyls (Witzmann and Soler-Gijón 2010) and many amniotes (e.g. Scheyer 2007 and references therein), the gastral and dorsal scales of limbed tetrapodomorphs, as well as basal tetrapods are periosteal and lack any components of metaplastic tissue.
7. The proportionally larger overlap surfaces of gastral scales indicate that the body of limbed tetrapodomorphs might have been more flexible than that of their finned relatives. This is also indicated by the mode of articulation of gastral scales in the ventral midline and by the thin dorsal scales in most forms. Also the nodal point could have contributed to an enhanced flexibility of the anterior trunk region and forelimbs.

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References

Ahlberg, P. E., Clack, J. A. and Blom, H. 2005. The axial skeleton of the Devonian tetrapod *Ichthyostega*. – *Nature* **437**: 137–140.

Anderson, J. S. 2003. A new aïstopod (Tetrapoda: Lepospondyli) from Mazon Creek, Illinois. – *Journal of Vertebrate Paleontology* **23**: 79–88.

Anderson, J. S., Reisz, R. R., Scott, D., Fröbisch, N. B. and Sumida, S. S. 2008. A stem batrachian from the Early Permian of Texas and the origin of frogs and salamanders. – *Nature* **453**: 515–518.

Beaumont, E. H. 1977. Cranial morphology of the Loxommatidae (Amphibia: Labyrinthodontia). – *Philosophical Transactions of the Royal Society of London* **280**: 29–101.

Berman, D. S. 1973. A trimerorhachid amphibian from the Upper Pennsylvanian of New Mexico. – *Journal of Paleontology* 47: 932–945.

Bickelmann, C., Müller, J. and Reisz, R. R. 2009. The enigmatic diapsid *Acerosodontosaurus piveteaui* (Reptilia: Neodiapsida) from the Upper Permian of Madagascar and the paraphyly of 'younginiform' reptiles. – *Canadian Journal of Earth Sciences* **46**: 651–661.

Boisvert, C. A. 2005. The pelvic fin and girdle of *Panderichthys* and the origin of tetrapod locomotion. – *Nature* **438**: 1145–1147.

Boisvert, C. A., Mark-Kurik, E. and Ahlberg, P. E. 2008. The pectoral fin of *Panderichthys* and the origin of digits. – *Nature* **456**: 636–638.

Bossy, K. A. and Milner, A. C. 1998. Order Nectridea. In Wellnhofer, P. (Ed.): *Encyclopedia of Paleoherpetology*, vol. 1: *Lepospondyli*, pp. 73–131. Verlag Friedrich Pfeil, München.

Boy, J. A. and Sues, H. D. 2000. Branchiosaurs: Larvae, Metamorphosis and Heterochrony in Temnospondyls and Seymouriamorphs. In Heatwole, H. and Carroll, R. L. (Eds): *Amphibian Biology*, vol. 4: *Palaeontology*, pp. 1150–1197. Surrey Beatty, Chipping Norton.

Brazeau, M. D. and Ahlberg, P. E. 2006. Tetrapod-like middle ear architecture in a Devonian fish. – *Nature* **439**: 318–321.

Broili, F. 1927. Über die Hautbedeckung der Archegosauridae und Actinodontidae. – *Zeitschrift der Deutschen Geologischen Gesellschaft* 79: 375–384.

Bulanov, V. 2003. Evolution and systematics of seymouriamorph parareptiles. – *Paleontological Journal* **37**, (Suppl 1) 1–105.

Bystrow, A. P. 1935. Morphologische Untersuchungen der Deckknochen des Schädels der Stegocephalen. 1. Mitteilung. Schadel der Stegocephalen. – *Acta Zoologica (Stockholm)* **16**: 65–141.

Bystrow, A. P. 1939. Zahnstruktur der Crossopterygier. – *Acta Zoologica (Stockholm)* **20**: 283–338.

Carroll, R. L. 1964. Early evolution of the dissorophid amphibians. – *Bulletin of the Museum of Comparative Zoology, Harvard University* **131**: 161–250.

Carroll, R. L. 1972. Gephyrostegida, Solenodonsauridae. In Kuhn, O. (Ed.): *Encyclopedia of Paleoherpetology*, vol. **5B**, *Batrachosauria*, pp. 1–19. Gustav Fischer Verlag, Stuttgart.

Carroll, R. L. 1995. Problems of the phylogenetic analysis of Paleozoic choanates. – *Bulletin du Muséum national d'Histoire naturelle de Paris, 4ème série* **17**: 389–445.

Carroll, R. L. 1998a. Order Microsauria. In Wellnhofer, P. (Ed.): *Encyclopedia of Paleoherpetology*, vol. 1: *Lepospondyli*, pp. 1–72. Verlag Dr. Friedrich Pfeil, München.

Carroll, R. L. 1998b. Order Aïstopoda. In Wellnhofer, P. (Ed.): *Encyclopedia of Paleoherpetology*, vol. 1: *Lepospondyli*, pp. 163–182. Verlag Dr. Friedrich Pfeil, München.

Carroll, R. L. 1998c. Order Undesignated [Family Acherontiscidae]. In Wellnhofer, P. (ed.): *Encyclopedia of Paleoherpetology*, vol. 1: *Lepospondyli*, pp. 183–185. Verlag Dr. Friedrich Pfeil, München.

Carroll, R. L. and Andrews, M. S. 1998. Order Adelospondyli. In Wellnhofer, P. (Ed.): *Encyclopedia of Paleoherpetology*, vol. 1: *Lepospondyli*, pp. 149–162. Verlag Dr. Friedrich Pfeil, München.

Carroll, R. L. and Baird, D. 1972. Carboniferous stem-reptiles of the family Romeriidae. – *Bulletin of the Museum of Comparative Zoology, Harvard University* **143**: 321–364.

Castanet, J., Francillon-Vieillot, H., Ricqlès, A. de. and Zylberberg, L. 2003. The Skeletal Histology of the Amphibia. In Heatwole, H. and Davies, M. (Eds): *Amphibian Biology*, vol. 5: *Osteology*, pp. 1598–1683. Surrey Beatty, Chipping Norton.

Chase, J. N. 1965. *Neldasaurus wrightae*, a new rhachitomous labyrinthodont from the Lower Permian. – *Bulletin of the Museum of Comparative Zoology Harvard University* **133**: 156–225.

Chinsamy, A. and Raath, M. A. 1992. Preparation of bone for histological study. – *Palaeontologia africana* **29**: 39–44.

Clack, J. A. 1987. *Pholiderpeton scutigerum* Huxley, an amphibian from the Yorkshire Coal Measures. – *Philosophical Transactions of the Royal Society of London* **318**: 1–107.

Clack, J. A. 1992. The Stapes of *Acanthostega gunnari* and the Role of the Stapes in Early Tetrapods. In Webster, D. B., Popper, A. N. and Fay, R. R. (Eds): *The Evolutionary Biology of Hearing*, pp. 405–420. Springer-Verlag, New York.

Clack, J. A. 1994. *Silvanerpeton miripedes*, a new anthracosauroid from the Viséan of east Kirkton, West Lothian, Scotland. – *Transactions of the Royal Society of Edinburgh, Earth Sciences* **84**: 369–376.

Clack, J. A. 1998. The neurocranium of *Acanthostega gunnari* Jarvik and the evolution of the otic region in tetrapods. – *Zoological Journal of the Linnean Society of London* **122**: 61–97.

Clack, J. A. 2001. *Eucritta melanolimnetes* from the early carboniferous of Scotland, a stem tetrapod showing a mosaic of characteristics. – *Transactions of the Royal Society of Edinburgh, Earth Sciences* **92**: 75–95.

Clack, J. A. 2002. *Gaining Ground. The Origin and Evolution of Tetrapods*. Indiana University Press, Bloomington.

Clack, J. A. 2006. The emergence of early tetrapods. – *Palaeogeography, Palaeoclimatology, Palaeoecology* **232**: 167–189.

Clack, J. A. 2009. The fin to limb transition: new data, interpretations, and hypotheses from paleontology and developmental biology. – *Annual Review of Earth and Planetary Sciences* **37**: 163–179.

Clack, J. A. and Finney, S. 2005. *Pederpes finneyae*, an articulated tetrapod from the Tournaisian of western Scotland. – *Journal of Systematic Palaeontology* **2**: 311–346.

Clack, J. A., Ahlberg, P. E., Finney, S. M., Dominguez Alonso, P., Robinson, J. and Ketcham, R. A. 2003. A uniquely specialized ear in a very early tetrapod. – *Nature* **425**: 65–69.

Claessens, L. P. A. M. 2004. Dinosaur gastralia; origin, morphology, and function. – *Journal of Vertebrate Paleontology* **24**: 89–106.

Coates, M. I. 1996. The Devonian tetrapod *Acanthostega gunnari* Jarvik: postcranial anatomy, basal tetrapod relationships and patterns of skeletal evolution. – *Transactions of the Royal Society of Edinburgh: Earth Sciences* **87**: 363–421.

Coates, M. I. and Clack, J. A. 1990. Polydactyly in the earliest known tetrapod limbs. – *Nature* **347**: 66–69.

Coates, M. I. and Clack, J. A. 1991. Fish-like gills and breathing in the earliest known tetrapod. – *Nature* **352**: 234–236.

Coates, M. I. and Clack, J. A. 1995. Romer's Gap Tetrapod Origins and Terrestriality. In Arsenault, M., Lelièvre, H. and Janvier, P. (Eds): *Studies on early vertebrates. Bulletin du Muséum national d'histoire naturelle, Paris*, pp. 373–388. Miguasha, Quebec.

Coates, M. I., Ruta, M. and Friedman, M. 2008. Ever since Owen: changing perspectives on the early evolution of tetrapods. – *Annual Reviews of Earth and Planetary Sciences* **39**: 571–592.

Colbert, E. H. 1955. Scales in the Permian amphibian *Trimerorhachis*. – *American Museum Novitates* **1740**: 1–17.

Cope, E. D. 1884. The Batrachia of the Permian period of North America. – *American Naturalist* **18**: 26–39.

Credner, H. 1881. Die Stegocephalen aus dem Rotliegenden des Plauen'schen Grundes bei Dresden. Zweiter Theil. – *Zeitschrift der Deutschen Geologischen Gesellschaft* **33**: 574–603.

Credner, H. 1886. Die Stegocephalen aus dem Rotliegenden des Plauen'schen Grundes bei Dresden. Sechster Theil. – *Zeitschrift der Deutschen Geologischen Gesellschaft* **38**: 567–633.

Credner, H. 1893. Die Stegocephalen aus dem Rotliegenden des Plauen'schen Grundes bei Dresden. Zehnter Theil. – *Zeitschrift der Deutschen Geologischen Gesellschaft* **45**: 639–704.

Daeschler, E. B., Shubin, N. H. and Jenkins, F. A. 2006. A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. – *Nature* **440**: 757–763.

Daeschler, E. B., Clack, J. A. and Shubin, N. H. 2009. Late Devonian tetrapod remains from Red Hill, Pennsylvania, USA: how much diversity? – *Acta Zoologica Stockholm* **90** (Suppl 1): 306–317.

DeMar, R. 1966. The phylogenetic and functional implications of the armor of the Dissorophidae. – *Fieldiana: Geology* **16**: 55–88.

DeMar, R. 1968. The Permian labyrinthodont amphibian *Dissorophus multicinctus*, and adaptations and phylogeny of the family Dissorophidae. – *Journal of Paleontology* **42**: 1210–1242.

Dias, E. V. and Richter, M. 2003. On the squamation of *Australerpeton cosgriffi* Barberena, a temnospondyl amphibian from the Upper Permian of Brazil. – *Anais da Academia Brasileira de Ciências* 74: 477–490.

Dilkes, D. 2009. Comparison and biomechanical interpretations of the vertebrae and osteoderms of *Cacops aspidephorus* and *Dissorophus multicinctus* (Temnospondyli, Dissorophidae). – *Journal of Vertebrate Paleontology* **29**: 1013–1021.

Dilkes, D. and Brown, L. E. 2007. Biomechanics of the vertebrae and associated osteoderms of the Early Permian amphibian *Cacops aspidephorus*. – *Journal of Zoology* **271**: 396–407.

Downs, J. P., Daeschler, E. B., Jenkins, F. A. and Shubin, N. H. 2008. The cranial endoskeleton of *Tiktaalik roseae*. – *Nature* **455**: 925–929.

Findlay, G. H. 1968. On the structure of the skin in *Uranocentrodon* (*Rhinesuchus*) *senekalensis* van Hoepen. – *Palaeontologia Africana* **11**: 15–22.

Francillon-Vieillot, H., de Buffrénil, V., Castanet, J., Geraudie, J., Meunier, F. J., Sire, J.-Y., Zylberberg, L. and de Ricqlès, A. 1990. Microstructure and Mineralization of Vertebrate Skeletal Tissues. In Carter, J. G. (Ed.): *Biomineralization: Patterns and Evolutionary Trends*, pp. 471–530. Van Nostrand Reinhold, New York.

Fritsch, A. 1883. *Fauna der Gaskohle und der Kalksteine der Permformation Böhmens*. Vol. **2**, Part 2. Selbstverlag, Praha.

Fritsch, A. 1889. *Fauna der Gaskohle und der Kalksteine der Permformation Böhmens*. Vol. **2**, Part 2. Selbstverlag, Praha.

Gemballa, S. and Bartsch, P. 2002. Architecture of the integument in lower teleostomes: functional morphology and evolutionary implications. – *Journal of Morphology* **253**: 290–309.

Godfrey, S. J. 1989a. The postcranial skeletal anatomy of the Carboniferous tetrapod *Greererpeton burkemorani* Romer 1969. – *Philosophical Transactions of the Royal Society of London* **323**: 75–133.

Godfrey, S. J. 1989b. Ontogenetic changes in the skull of the Carboniferous tetrapod *Greererpeton burkemorani* Romer 1969. – *Philosophical Transactions of the Royal Society of London* **323**: 135–153.

Golubev, V. K. 1998. Narrow-armored chroniosuchians (Amphibia, Anthracosauromorpha) from the Late Permian of Eastern Europe. – *Paleontological Journal* **32**: 278–287.

Gross, W. 1930. Die Fische des mittleren Old Red Süd-Livlands. – *Geologische und Paläontologische Abhandlungen* **22**: 123–156.

Gross, W. 1966. Kleine Schuppenkunde. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **125**: 29–48.

Hellrung, H. 2003. *Gerrothorax pustuloglomeratus*, ein Temnospondyle (Amphibia) mit knöcherner Branchialkammer aus dem Unteren Keuper von Kupferzell (Süddeutschland). – *Stuttgarter Beiträge zur Naturkunde, Serie B* **330**: 1–130.

Holmes, R. 1984. The Carboniferous amphibian *Proterogyrinus scheelei* Romer, and the early evolution of tetrapods. – *Philosophical Transactions of the Royal Society of London* **306**: 431–524.

Hook, R. W. 1983. *Colosteus scutellatus* (Newberry), a primitive temnospondyl amphibian from the Middle Pennsylvanian of Linton, Ohio. – *American Museum of Natural History Novitates* **2770**: 1–41.

Huxley, T. H. 1862. On new labyrinthodonts from the Edinburgh coal field. – *Proceedings of the Geological Society of London* **1862**: 291–296.

Ivakhnenko, N. 1987. Permian parareptiles of the Soviet Union. – *Trudy Paleontologiceskogo Instituta SSSR* **223**: 1–158. [In Russian].

Janvier, P. 1992. Les écailles des Trématosaures (Tetrapoda, Temnospondyli): nouvelles données sur les Trématosaures du Trias inférieur de Madagascar. – *Bulletin Du Musée National d'Histoire Naturelle, Paris, 4e Série* **14**: 3–13.

Janvier, P. 1996. *Early Vertebrates*. Oxford University Press, Oxford.

Jarvik, E. 1948. On the morphology and taxonomy of the Middle Devonian osteolepid fishes of Scotland. – *Kungliga Svenska Vetenskapsakademiens Handlingar, Tredje Serien* **25**: 1–301.

Jarvik, E. 1952. On the fish-like tail in the ichthyostegid stegocephalians with descriptions of a new stegocephalian and a new crossopterygian from the Upper Devonian of East Greenland. – *Meddelelser Om Grønland* **114**: 1–90.

Jarvik, E. 1980. *Basic Structure and Evolution of Vertebrates*, vol. **1**. Academic Press, London.

Jenkins, F. A., Shubin, N. H., Gatesy, S. M. and Warren, A. 2008. *Gerrothorax pulcherrimus* from the Upper Triassic Fleming Fjord Formation of east Greenland and a reassessment of head lifting in temnospondyl feeding. – *Journal of Vertebrate Paleontology* **28**: 935–950.

Jessen, H. 1972. Die Bauchschuppen von *Moythomasia nitida* Gross (Pisces, Actinopterygii). – *Paläontologische Zeitschrift* **46**: 121–132.

Kerr, T. 1952. The scales of primitive living actinopterygians. – *Proceedings of the Zoological Society of London* **122**: 55–78.

Klembara, J. and Bartík, I. 2000. The postcranial skeleton of *Discosauriscus* Kuhn, a seymouriamorph tetrapod from the Lower Permian of the Boskovice Furrow (Czech Republic). – *Transactions of the Royal Society of Edinburgh, Earth Sciences* **90**: 287–316.

Klembara, J. and Ruta, M. 2004. The seymouriamorph tetrapod *Utegenia shpinari* from the ?Upper Carboniferous–Lower Permian of

Kazakhstan. Part II: Postcranial anatomy and relationships. – *Transactions of the Royal Society of Edinburgh, Earth Sciences* **94**: 75–93.
Konzhukova, E. D. 1955. *Platyops stuckenbergi* Trautschold – an archegosaurid from the lower zone of the Upper Permian in the Ural region. – *Trudy Paleontologichesko Instituta* **49**: 89–127. [in Russian].
Laurin, M. 1996. A reappraisal of *Utegenia*, a Permo-Carboniferous seymouriamorph (Tetrapoda, Batrachosauria) from Kazakhstan. – *Journal of Vertebrate Paleontology* **16**: 374–383.
Laurin, M. and Reisz, R. R. 1997. A New Perspective on Tetrapod Phylogeny. In Sumida, S. S. and Martin, K. (Eds): *Amniote Origins – Completing the Transition to Land*, pp. 9–59. Academic Press, London.
Laurin, M. and Reisz, R. R. 1999. A new study of *Solenodonsaurus janenschi*, and a reconsideration of amniote origins and stegocephalian evolution. – *Canadian Journal of Earth Sciences* **36**: 1239–1255.
Lebedev, O. A. and Coates, M. I. 1995. The postcranial skeleton of the Devonian tetrapod *Tulerpeton curtum* Lebedev. – *Zoological Journal of the Linnean Society* **114**: 307–348.
Lombard, R. E. and Bolt, J. R. 1995. A new primitive tetrapod, *Whatcheeria deltae*, from the Lower Carboniferous of Iowa. – *Palaeontology* **38**: 471–494.
Meyer, H. von. 1858. Reptilien aus der Steinkohlenformation in Deutschland. – *Palaeontographica* **6**: 59–219.
Milner, A. C. and Lindsay, W. 1998. Postcranial remains of *Baphetes* and their bearing on the relationships of the Baphetidae (= Loxommatidae). – *Zoological Journal of the Linnean Society* **122**: 211–235.
Milner, A. C., Milner, A. R. and Walsh, S. A. 2009. A new specimen of *Baphetes* from Nýřany, Czech Republic and the intrinsic relationships of the Baphetidae. – *Acta Zoologica (Stockholm)* **90** (special issue): 318–334.
Niedźwiedzki, G., Szrek, P., Narkiewicz, K., Narkiewicz, M. and Ahlberg, P. E. 2010. Tetrapod trackways from the early Middle Devonian period of Poland. – *Nature* **463**: 43–48.
Nilsson, T. 1946. A new find of *Gerrothorax rhaeticus* Nilsson, a plagiosaurid from the Rhaetic of Scania. – *Lunds Universitets Årsskrift, Ny Följd* **42**: 1–43.
Novikov, I. V., Shishkin, M. A. and Golubev, V. K. 2000. Permian and Triassic Anthracosaurs from Eastern Europe. In Benton, M., Shishkin, M. A., Unwin, D. and Kurochkin, E. (Eds): *The Age of Dinosaurs in Russia and Mongolia*, pp 60–70. Cambridge University Press, Cambridge.
Olson, E. C. 1979. Aspects of the biology of *Trimerorhachis* (Amphibia: Temnospondyli). – *Journal of Paleontology* **53**: 1–17.
Panchen, A. 1959. A new armoured amphibian from the Upper Permian of East Africa. – *Philosophical Transactions of the Royal Society of London, Series B* **242**: 207–281.
Panchen, A. L. 1970. *Anthracosauria*. In Kuhn, O. (Ed.): *Encyclopedia of Paleoherpetology*, vol. **5A**: *Batrachosauria*, pp. 1–82. Gustav Fischer Verlag, Stuttgart.
Panchen, A. L. 1975. A new genus and species of anthracosaurs amphibian from the Lower Carboniferous of Scotland and the status of *Pholidogaster pisciformis* Huxley. – *Philosophical transactions of the Royal Society of London* **269**: 581–640.
Panchen, A. L. 1985. On the amphibian *Crassigyrinus scoticus* Watson from the Carboniferous of Scotland. – *Philosophical transactions of the Royal Society of London* **309**: 505–568.
Romer, A. S. 1956. *Osteology of the Reptiles*. University of Chicago Press, Chicago.
Romer, A. S. 1964. The skeleton of the Lower Carboniferous labyrinthodont *Pholidogaster pisciformis*. – *Bulletin of the Museum of Comparative Zoology, Harvard University* **131**: 129–159.
Romer, A. S. 1972. A Carboniferous labyrinthodont amphibian with complete dermal armor. – *Kirtlandia* **16**: 1–8.
Romer, A. S. and Witter, R. V. 1941. The skin of the rhachitomous amphibian *Eryops*. – *American Journal of Sciences* **239**: 822–824.
Ruta, M. and Coates, M. I. 2007. Dates, nodes and character conflict: addressing the lissamphibian origin problem. – *Journal of Systematic Paleontology* **5**: 69–122.
Ruta, M., Coates, M. I. and Quicke, D. L. J. 2003a. Early tetrapod relationships revisited. – *Biological Reviews* **78**: 251–345.
Ruta, M., Jeffery, J. E. and Coates, M. I. 2003b. A supertree of early tetrapods. – *Proceedings of the Royal Society of London* **270**: 2507–2516.
Scheyer, T. M. 2007. Skeletal histology of the armor of the Placodontia: the occurrence of 'postcranial fibro-cartilaginous bone' and its developmental implications. – *Journal of Anatomy* **211**: 737–753.
Schoch, R. R. 2003. Early larval ontogeny of the Permo-Carboniferous temnospondyl *Sclerocephalus*. – *Palaeontology* **46**: 1055–1072.
Schultze, H.-P. 1966. Morphologische und histologische Untersuchungen an Schuppen mesozoischer Actinopterygier (Übergang von Ganoid- zu Rundschuppen). – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **126**: 232–314.
Schultze, H.-P. 1977. Ausgangsform und Entwicklung der rhombischen Schuppen der Osteichthyes (Pisces). – *Paläontologische Zeitschrift* **51**: 152–168.
Schultze, H.-P. 1996. The Elpistostegid Fish *Elpistostege*, the Closest the Miguasha fauna Comes to a Tetrapod. In Schultze, H.-P. and Cloutier, R. (Eds): *Devonian Fishes and Plants of Miguasha, Quebec, Canada*, pp. 316–327. Verlag Dr. Friedrich Pfeil, München.
Schultze, H.-P. 1997. Umweltbedingungen beim Übergang von Fisch zu Tetrapode [Paleoenvironment at the transition from fish to tetrapod]. – *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* **36**: 59–77.
Schultze, H.-P. and Arsenault, M. 1985. The panderichthyid fish *Elpistostege*: a close relative of tetrapods? – *Palaeontology* **28**: 293–309.
Shubin, N. H., Daeschler, E. B. and Jenkins, F. A. 2006. The pectoral fin of *Tiktaalik rosae* and the origin of the tetrapod limb. – *Nature* **440**: 764–771.
Sire, J.-Y. and Akimenko, M.-A. 2004. Scale development in fish: a review, with description of sonic *hedgehog (shh)* expression in the zebrafish (*Danio rerio*). – *International Journal of Developmental Biology* **38**: 233–247.
Sire, J.-Y., Donoghue, P. C. J. and Vickaryous, M. K. 2009. Origin and evolution of the integumentary skeleton in non-tetrapod vertebrates. – *Journal of Anatomy* **214**: 409–440.
Smithson, T. R. 1982. The cranial morphology of *Greererpeton burkemorani* Romer (Amphibia: Temnospondyli). – *Zoological Journal of the Linnean Society of London* **76**: 29–90.
Smithson, T. R. 1994. *Eldeceeon rolfei*, a new reptiliomorph from the Visean of East Kirkton, West Lothian, Scotland. – *Transactions of the Royal Society of Edinburgh, Earth Sciences* **84**: 377–382.
Špinar, Z. V. 1952. Revision of some Moravian Discosauriscidae (Labyrinthodontia). – *Rozpravy ÚÚG* **15**: 1–115. [In Czech].
Vallin, G. and Laurin, M. 2004. Cranial morphology and affinities of *Microbrachis*, and a reappraisal of the phylogeny and lifestyle of the first amphibians. – *Journal of Vertebrate Paleontology* **24**: 56–72.
Vickaryous, M. K. and Sire, J.-Y. 2009. The integumentary skeleton of tetrapods: origin, evolution, and development. – *Journal of Anatomy* **214**: 441–464.
Vorobyeva, E. I. and Schultze, H.-P. 1991. Description and Systematics of Panderichthyid Fishes with Comments on Their Relationship to Tetrapods. In Schultze, H.-P. and Trueb, L. (Eds): *Origins*

of Higher Groups of Tetrapods, pp. 68–109. Comstock Publishing Associates, Ithaca.

Witzmann, F. 2007. The evolution of the scalation pattern in temnospondyl amphibians. – *Zoological Journal of the Linnean Society London* **150**: 815–834.

Witzmann, F. and Soler-Gijón, R. 2010. The bone histology of osteoderms in temnospondyl amphibians and in the chroniosuchian *Bystrowiella*. – *Acta Zoologica (Stockholm)* **91**: 96–114.

Witzmann, F., Schoch, R. R. and Maisch, M. 2008. A relict basal tetrapod from Germany: first evidence of a Triassic chroniosuchian outside Russia. – *Naturwissenschaften* **95**: 67–72.

Witzmann, F., Scholz, H., Müller, J. and Kardjilov, N. 2010. Sculpture and vascularization of dermal bones, and the implications for the physiology of basal tetrapods. – *Zoological Journal of the Linnean Society*. In press.

The hyobranchial apparatus in early tetrapods and its significance for feeding and breathing

Appendix 10

Witzmann, F. 2013. Phylogenetic patterns of character evolution in the hyobranchial apparatus of early tetrapods. – Earth and Environmental Science Transactions of the Royal Society of Edinburgh 104, 145–167.

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Phylogenetic patterns of character evolution in the hyobranchial apparatus of early tetrapods

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ABSTRACT: The morphologies of the hyobranchial apparatus in early tetrapods are reviewed, based primarily on first-hand examination and supplemented by published descriptions. The basic arrangement of the "aquatic" hyobranchium, with four pairs of branchial arches and internal gills, was conserved to a remarkable degree across the fish–to–tetrapod transition and was retained in further evolution in adults of several tetrapod lineages. Thus, a fish-like hyobranchium in basal tetrapods does not necessarily represent a larval or paedomorphic character, respectively, as was often suggested in analogy to extant salamanders. Rather, it represents the plesiomorphic state of the adult hyobranchium in tetrapods. The changes in the hyobranchium during the fish–to–tetrapod transition include the reduction of the number of skeletal elements and their morphological simplification. In all three presently discussed scenarios of lissamphibian origin, the temnospondyl, lepospondyl and diphyly hypotheses, the internal gills were reduced independently within temnospondyls and on the amniote stem below seymouriamorphs. Evidence of remodelling into a true "terrestrial" hyobranchium, with reduction of the posterior branchial arches and modification to support terrestrial tongue feeding, is scarce in early tetrapods. It evolved within temnospondyls in zatracheids, amphibamids and lissamphibians, as well as once or several times in early amniotes or in their immediate stem-forms.

KEY WORDS: Branchial arches, fish–to–tetrapod transition, gills, gill skeleton, Lepospondyli, Mesozoic, Palaeozoic, stem-tetrapods, Temnospondyli

The hyobranchial or visceral skeleton of gnathostomes plays a fundamental role in breathing and feeding. In gnathostome fishes and aquatic amphibians, movements of the apparatus assist in opening the jaws and expanding the bucco-pharyngeal cavity, thus generating negative pressure within the mouth cavity and initiating a rapid inflow of water together with the prey, a mechanism that is referred to as suction feeding (e.g., Lauder & Reilly 1994). The hyobranchial skeleton shows a wide variety of morphologies and characteristics among the different lineages and taxa of gnathostome fishes and tetrapods. The 'generalised' or plesiomorphic configuration of the hyobranchial skeleton is a complex set of paired segmented arches, consisting of the mandibular arch (i.e., the jaws), followed by the hyoid arch and the subsequent branchial (or gill) arches, which are linked ventrally to the median basibranchial series (Nelson 1969; Janvier 1996). The anteriormost element of the basibranchial series is usually referred to as basihyal and is connected with the hyoid arch; the posteriorly-following elements of the series are the basibranchials which are associated with the branchial arches. Whereas the mandibular arch consists of only two segments (the palatoquadrate dorsally and the Meckelian cartilage ventrally), the hyoid arch can be subdivided into the hypohyal, the ceratohyal and the hyomandibula (from ventral to dorsal). One or two small bones might be interconnected between the ceratohyal and the hyomandibular in osteichthyan fishes, the symplectic and the interhyal (Janvier 1996). The posteriorly-following branchial arches are plesiomorphically five in number, but may vary from one to six in gnathostome fishes and tetrapods. The following segments can be distinguished per branchial arch (from ventral to dorsal): hypo-, cerato-, epi- and pharyngobranchial (divided into infra- and supraphar-yngeal) (Fig. 1). The gills (either external or internal gills or both) are attached to the branchial arches. During the fish–to–tetrapod transition and the subsequent conquest of land by vertebrates in the Late Palaeozoic, the hyobranchial apparatus of fishes had to be remodelled during the change from an aquatic to a rather terrestrial existence, in order to perform terrestrial feeding. Furthermore, the hyobranchial skeleton had to facilitate an increasing amount of aerial respiration, with a corresponding decrease in the importance of gill breathing. Better knowledge of the transformation of the hyobranchial apparatus during the fish–to–tetrapod transition and its further evolution in basal tetrapods is thus crucial for understanding early tetrapod history and the adaptations to life on land.

Coates & Clack (1991) and Clack *et al.* (2003) showed that the Late Devonian stem-tetrapods *Acanthostega* and *Ichthyostega* have a hyobranchial skeleton that closely resembles those of bony fishes. They discovered osteological correlates of internal gills, such as three or four pairs of ossified ceratobranchials with grooves for gill arch arteries, and a cleithrum (or clavicle) that bears a medially directed postbranchial lamina. In osteichthyan fishes, this lamina forms the posterior wall of the opercular chamber (Coates & Clack 1991). A hyobranchial skeleton with similar three or four pairs of ceratobranchials has been demonstrated in a variety of adult aquatic basal tetrapods from the Permo-Carboniferous and the Triassic (Bystrow 1938; Nilsson 1946; Wellstead 1991; Andrews & Carroll 1991; Schoch 2002; Hellrung 2003; Jenkins *et al.* 2008). Schoch & Witzmann (2011) showed that most of these aquatic forms possessed the osteological correlates of internal gills similar to the Devonian forms, whereas their larvae bore external gills resembling those of extant salamander larvae. The adult hyobranchial apparatus

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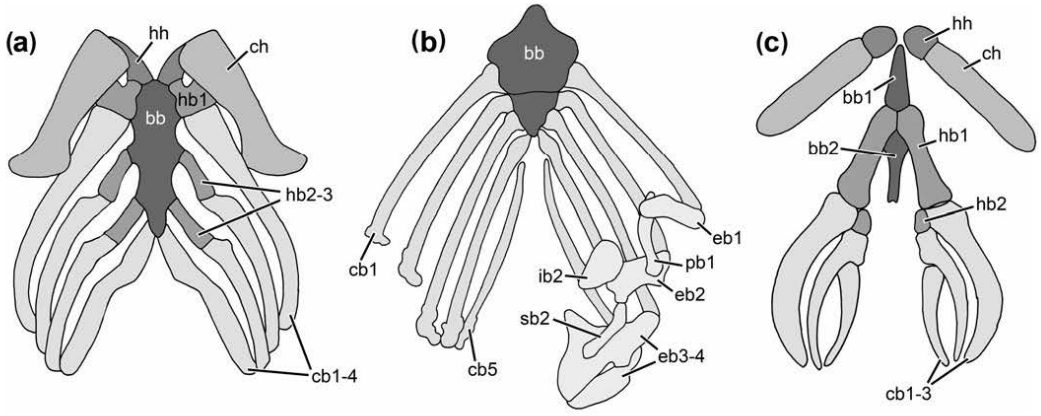

Figure 1 Hyobranchial skeletons of extant actinopterygians and sarcopterygians: (a) the actinopterygian *Polypterus*; distal arch elements are omitted (redrawn from Nelson 1969); (b) the coelacanth *Latimeria*; distal arch elements are omitted on the left side (redrawn from Forey 1998); (c) the paedomorphic salamander *Necturus* (redrawn from Stadtmüller 1936). Abbreviations: bb = basibranchial; cb = ceratobranchial; ch = ceratohyal; eb = epibranchial; hb = hypobranchial; hh = hypohyal; ib = infrapharyngobranchial; pb = pharyngobranchial; sb = suprapharyngobranchial.

of more terrestrial basal tetrapods such as eryopid, zatracheid and dissorophoid temnospondyls or "microsaurs", on the other hand, is poorly known, and only a few descriptions of rather fragmentary elements exist (Romer 1969; Boy 1985; Witzmann & Schoch 2006; Clack & Milner 2010). In contrast, the larval hyobranchium of many of these forms is well known based on the presence of ossified or cartilaginous branchial arches often associated with branchial dentition and external gills (Boy 1974; Boy & Sues 2000; Witzmann 2004; Milner 2007; Schoch & Milner 2008).

Although a large number of thorough osteological descriptions of basal tetrapods do exist, the majority of these studies are concentrated on the skull and on the postcranium, but deal only superficially with the morphology and the phylogenetic alteration of the hyobranchial skeleton. This may be due to the fact that the sometimes tiny and feebly ossified hyobranchial skeletal elements of early tetrapods are often poorly preserved and are thus difficult to interpret. However, numerous new finds of hyobranchial elements in recent years allow for a detailed investigation of these bones. In the following study, the hyobranchial morphologies of early tetrapods are reviewed, based primarily on first-hand examination and supplemented by published descriptions. This study will focus on those parts of the hyobranchial apparatus that can anatomically be compared between taxa. The following questions will be settled. What is the plesiomorphic condition of the hyobranchial apparatus in tetrapods, and which phylogenetic signals can be recovered in hyobranchial morphologies of the different tetrapod lineages? Can "terrestrial" and "aquatic" hyobranchial apparatus be distinguished in early tetrapods, and in which taxa can internal gills be assumed, based on the osteological correlates used by Coates & Clack (1991) and Schoch & Witzmann (2011)? This study may further serve as a basis for later functional analyses of breathing and feeding in early tetrapods based on hyobranchial morphology.

1. Phylogenetic framework and general comments on hyobranchial morphology

In the present study, the phylogenetic results of Ruta & Coates (2007) and Schoch (2013) are taken as phylogenetic framework of early tetrapod interrelationships. The term 'basal tetrapod' is accordingly used for non-amniote crown-group tetrapods of the Palaeozoic and Mesozoic. Among them, temnospondyls are regarded as the clade that includes all groups of lissamphibians, and "anthracosaurs" (including seymouriamorphs) and lepospondyls are regarded as stem-amniotes. Devonian forms, as well as colosteids, adelogyrinids and baphetids, are referred to as stem-tetrapods. Basal tetrapods and stem-tetrapods are informally designated here as "early tetrapods". For an alternative view of early tetrapod relationships, see Marjanović & Laurin (2008, and references therein).

"Proximal" is used here to refer to the portion of a hyobranchial element that is close to the basibranchial (i.e. to the ventral midline), whereas "distal" refers to the opposite direction. This appears to be clearer than to use "ventral" and "dorsal", respectively, as is sometimes done, since the distal ends of certain hyobranchial elements are often located laterally rather than dorsally with respect to the proximal parts.

Identification of hyobranchial elements is often difficult in fossil specimens because of the frequently poor and incomplete state of preservation. Many excellently preserved specimens of stem-tetrapods and basal tetrapods, however, such as *Acanthostega*, dvinosaurians, plagiosaurids, branchiosaurids, adelogyrinids, etc., have the hyobranchial apparatus almost completely ossified and articulated. The knowledge of the morphology and configuration of the hyobranchial apparatus in these forms enables comparison with fragmentary hyobranchia, or even isolated elements in other taxa, and their identification. In contrast to most gnathostome fishes that possess a number of basibranchial elements in the ventral midline of the hyobranchium (Nelson 1969; Janvier 1996), only one unpaired basibranchial bone is known in basal tetrapods (sometimes also called the copula, Boy 1974), which is located normally ventral to the parasphenoid. Elements of the hyoid arch can be distinguished from those of the branchial arches as follows. Hypohyals are usually rather small, (elongate) rectangular and located anterolateral to the anterior tip of the basibranchial. The ceratohyals are located distal to the hypohyals. When fully ossified, they are normally the longest elements of the hyobranchial skeleton. Generally, they have a flattened and often blade-like morphology. The hyomandibula of bony fishes has already

transformed to the stapes in stem-tetrapods; although initially part of the hyobranchial skeleton, the stapes will not be considered here, since it became independent from the hyoid arch in tetrapods and attained a completely new functional role (Clack 1992). Hypobranchials form the proximal part of the branchial arches and are rod-like bones located lateral and posterolateral to the basibranchial. They are mostly straight and rather short. Distal to them are the much longer ceratobranchials that are most often slightly curved. Posterolateral grooves for the branchial arteries on the ceratobranchials may indicate the presence of fish-like internal gills (Coates & Clack 1991; Schoch & Witzmann 2011), whereas ceratobranchials without grooves may have borne external gills or no gills at all. Hyobranchial skeletal elements in early tetrapods always have unfinished ends, i.e. they were usually continued in cartilage to a certain degree.

Reilly & Lauder (1988) demonstrated on the basis of comparative osteology and myology that it is most parsimonious to designate the proximal-most elements in the salamander branchial arches as hypobranchials and the distally following segments as ceratobranchials. This interpretation is followed here in the description of basal tetrapod hyobranchia, whose basic configuration of skeletal elements corresponds to that in larval salamanders. This view is in accordance with most authors who studied fossil tetrapod hyobranchia, e.g. Bystrow (1938), Boy (1974), Andrews & Carroll (1991), Coates & Clack (1991), Witzmann (2004) and Schoch & Witzmann (2011); but in contrast to Sushkin (1936), Romer (1969), Carroll & Gaskill (1978) and Wellstead (1991), who preferred the usage of the terms ceratobranchial and epibranchial for the two proximal-most segments of branchial arches.

If one or more particular hyobranchial elements are not preserved in any known specimen of a certain early tetrapod taxon, it might be assumed that the respective element(s) were cartilaginous in life. A fundamental problem in analysing the hyobranchial skeleton of early tetrapods, however, is how the failure of a cartilaginous element to fossilise is distinguished from the evolutionary loss or absence of the element in question. This problem becomes even worse if one considers, for example, the extensive variation in ossification patterns of the hyobranchium in extant salamanders. This problem will be addressed below in the discussion paragraph. A further problem is that many of the hyobranchial elements of early tetrapods are very small and might easily get lost after the death of the animal and are therefore simply not preserved.

Early growth stages (or larvae) are distinguished from adult stem- and basal tetrapods by the presence of external gills, which are a larval characteristic at least in temnospondyls (and extant amphibians) and seymouriamorphs (Witzmann 2004). However, since direct preservation of gills is rather exceptional, the existence of dentigerous branchial platelets, which in life would be attached to the branchial arches and indicate opened gill clefts, *plus* an overall poor degree of ossification of the endocranial and postcranial skeleton (especially vertebral centra, pelvis, and carpals and tarsals), are considered to indicate a larval form and distinguish it from an adult one.

2. Material studied

The following specimens were investigated for the present study:

Tetrapodomorph fishes. *Eusthenopteron foordi* (Late Devonian), NRM PZ 2609.

Stem-tetrapods. *Acanthostega gunnari* (Late Devonian), MGUH f.n.1227, f.n.1300; *Greererpeton burkemorani* (Middle and Late Carboniferous), CMNH 11090, 11130, 11219, 11132, 11073, 11320; Adelogyrinidae (Early Carboniferous), *Adelogyrinus simorhynchus*: NMS.G.1889.101.17; *Adelospondylus watsoni*, NMS.G.1885.57.51.

Temnospondyli. *Dvinosaurus* (Late Permian): *D. primus*, PIN 2005/39, Am/40, Am/41; *D. campbelli*, PIN 4818/410; PIN uncatalogued (several isolated ceratobranchials); *Trimerorhachis insignis* (Early Permian), UCMP 105175, 154434, 105146, 105221, 105163, 142027; *Tabanchuia oomie* (Early Triassic), UCMP 42777, 42781, 42780; *Isodectes obtusus* (Early Permian), AMNH 11037; *Branchierpeton amblystomum* (Early Permian), MMG SaP 179, MNC-F 10368; *Apateon gracilis* (Early Permian), MB.Am.406; *Micropholis stowi* (Early Triassic), BSM 1934 VIII 43; *Platyrhinops lyelli* (Late Carboniferous), MB.Am.23, 331; *Iberospondylus schultzei* (Late Carboniferous), PU-ANF 14; *Sclerocephalus* (Permo-Carboniferous), *S. haeuseri*: BSM AS I 575, SMNS 81791, 91800, MB.Am.1309, UHC-P 0489; *S. nobilis*, NHMM-PW 2005/2; *Glanochthon* (Early Permian), *G. latrirostris*: MB.Am.211; *G. angusta*, GPIT.Am.34; *Archegosaurus decheni* (Early Permian), MB.Am.983, IGS U II $^{1}/_{2}$; *Lydekkerina huxleyi* (Early Triassic), BSM 1934 VIII 44; *Stanocephalosaurus birdi (Wellesaurus peabodyi)*, UCMP 56098, 36040; *Trematolestes hagdorni* (Middle Triassic), SMNS 81790; *Callistomordax kugleri* (Middle Triassic), SMNS 90700; *Metoposaurus diagnosticus* (Middle Triassic), SMNS 5143; *Gerrothorax pulcherrimus* (Middle Triassic), SMNS 83866, 83382, MGUH 28919, NRM-PZ B.18b; *Plagiosuchus pustuliferus* (Middle Triassic), SMNS 84794.

Lepospondyli. *Microbrachis pelikani* (Late Carboniferous), AMNH 2557.

Seymouriamorpha. *Ariekanerpeton sigalovi* (Early Permian), PIN 2079/35, 41, 53, 117, 450, 563, 566, 601, 630, 631, 645, 679, 719, 755, 815.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; BSM, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; CMNH, Cleveland Museum of Natural History, Cleveland / Ohio, USA; GPIT, Institut und Museum für Geologie und Paläontologie Tübingen, Germany; IGS, Institut de Géologie Strasbourg, Université Louis Pasteur, France; MB, Museum für Naturkunde Berlin, Germany; MGUH, Geological Museum, University of Copenhagen, Denmark; MMG SaP, Museum für Mineralogie und Geologie zu Dresden, Germany, Sachsen-Perm-Sammlung; MNC, Museum für Naturkunde Chemnitz, Germany; NHMM, Naturhistorisches Museum Mainz, Germany; NMS, National Museums of Scotland, Edinburgh, UK; NRM, Naturhistoriska riksmuseet Stockholm, Sweden; PIN, Paleontological Institute and Museum of the Russian Academy of Science, Moscow, Russia; PU-ANF, Departamento de Paleontología, Universidad Complutense, Madrid, Spain; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UCMP, Museum of Paleontology of the University of California, Berkeley, USA; UHC-P, Ulrich Heidtke Collection, Paläontologische Sammlung, Niederkirchen, Germany.

3. Description

3.1. Stem-tetrapods

3.1.1. *Acanthostega*. The largest preserved hyobranchial elements in *Acanthostega gunnari* are the ceratohyals (Fig. 2a). The left ceratohyal is well preserved in MGUH f.n.1227 and is exposed in ventro-lateral view. Coates & Clack (1991) suggested that it had rotated around 180° compared to its original orientation and swapped sides. However, the shape of the ceratohyal in *Tiktaalik* (Downs *et al.* 2008, fig. 6) and in *Trimerorhachis* (see below) suggests that the preserved orientation is

correct. The ceratohyal is approximately 1.2 times longer than the ceratobranchials. Its proximal end is rounded and flattened, whereas the distal end is tapering. At mid-length, the anterodorsal margin bears a knob-like expansion with a distal "notch", from which an anterodorsal crest runs towards the distal tip of the ceratohyal. A conspicuous ridge (medial ridge *sensu* Coates & Clack 1991) extends parallel to the posteroventral margin from the expanded proximal blade in a distal direction. It exhibits fan-shaped striae in its proximal region that can be interpreted as muscle scars (Fig. 2a). This ridge is connected to the smaller anterodorsal crest via a short, transversally aligned crest.

Anteromedial to the ceratohyals is a pair of small, squarish bones in MGUH f.n.1227. Their margins are ill-defined and the elements seem to be crushed, thus indicating a poor degree of ossification in the living animal. Their small size and anteromedial location indicate that these elements are hypohyals (see also Coates & Clack 1991).

Coates & Clack (1991) did not comment on the number of ceratobranchials in *Acanthostega*, whereas Clack & Coates (1993) restored its hyobranchial skeleton with three ceratobranchials per side. This was reproduced in Clack (2012). Re-examination of the gill skeleton showed that four pairs of ossified ceratobranchials are present in *Acanthostega*. As discovered by Coates & Clack (1991), their posterolateral surface bears a deep groove whose width corresponds almost to the width of the ceratobranchial and is visible along the whole length of the element (Fig. 2a). At their proximal end, the ceratobranchials bear two blunt processes and are slightly wider than at the distal tip. Distal (dorsal) to left ceratobranchial 4 in MGUH f.n.1227 is a short rod-like element that can be interpreted as epibranchial (see also Clack & Coates 1993 and Clack 2012). Clack *et al.* (2003) discovered similar grooved branchial arches in the Devonian stem-tetrapod *Ichthyostega*.

3.1.2. Adelospondyli: *Adelogyrinus*. The ceratohyals are the largest and broadest elements of the hyobranchium (Fig. 2b) in the only known specimen of *Adelogyrinus simorhynchus* (NMS.G.1889.101.17). Their proximal and distal ends are broadened, and the shaft is curved and laterally convex and bears no processes. Five further elements can be interpreted as hypobranchials according to their location and orientation (Fig. 2b); thus, at least three pairs of hypobranchials were present in the living animal, as already reconstructed by Andrews & Carroll (1991). The first pair is the stoutest, with the distal end being broader than the proximal one, and the posterior edge being more concave than the anterior one. The second and third pairs are more slender, but have otherwise similar proportions.

Four or five long, slender ceratobranchials can be recognised distal to the hypobranchials (Fig. 2b). One element of the first pair is preserved dorsal to the first hypobranchials. The bone is bent and slightly broader proximally than distally. Crests or grooves are not visible. The second pair of ceratobranchials is preserved dorsal to the second pair of hypobranchials. These bones are straight, and the left one has a posterolateral groove that extends along almost its entire length; near the proximal end of the bone, the groove curves posteriorly and medially and becomes untraceable. One ceratobranchial of the third pair is preserved dorsal to the third pair of hypobranchials. The proximal portion of the element is concealed by the interclavicle. The posterolateral surface of the distal portion is slightly concave, and a distinct crest is visible laterally on the shaft that delimits a posterior groove on the ceratobranchial. Posterior to this element, a small part of a bone is visible, most of which is overlain by the interclavicle. It might represent the second element of the third pair of ceratobranchials. According to this description, *Adelogyrinus* has three pairs of ossified ceratobranchials (*contra* two pairs *sensu* Andrew & Carroll 1991), and at least the second and third pairs of them bear posterolateral grooves.

3.1.3. Adelospondyli: *Adelospondylus*. An isolated, curved bone that is associated with *Adelospondylus watsoni*, specimen NMS.G.1885.57.51, is broadened at one end and tapers continuously towards the other end (Fig. 2c, d). It is ovate in cross-section. The surface of the more slender portion bears numerous striae that might represent muscle scars. The convex edge of this curved bone bears a groove that diminishes towards the broadened end. This bone, although conspicuously smaller, closely resembles the ceratobranchials in *Dvinosaurus* (see below). If the interpretation as a ceratobranchial is correct, then the broadened part represents the proximal end of the bone.

3.1.4. Colosteidae: *Greererpeton*. In *Greererpeton burkemorani* (CMNH 11090), the anterior part of the rod-like basibranchial attains more than five times the width of the slender shaft and is diamond-shaped (Fig. 2e). The ventral surface of the broadening is slightly convex, with a narrow concave part lateral to it. The basibranchial is not bent in lateral view. The shaft bears a ventral keel or crest, which diminishes anteriorly on the broadened portion. In CMNH 11130, it is clearly visible that the basibranchial is broadened also in its posterior part, attaining approximately two thirds the width of the anterior portion (Fig. 2f). In CMNH 11219, two or three short, stout rod-like bones are present posterolateral to the basibranchial and might represent remains of hypobranchials.

Dentigerous branchial platelets that were attached to the cartilaginous ceratobranchials in the living animal can be found in two adult skulls and a juvenile (CMNH 11219, 11320, 11132). These platelets are elongated, ovate in outline and bear one row of approximately 20 teeth at the bulge-like, presumably posterior margin (Fig. 2g). The internal surface of the platelets is concave. Due to incomplete preservation, it cannot be ascertained how many rows of platelets were present.

3.1.5. Colosteidae: *Colosteus*. Hook (1983, fig. 7a) figured short, rod-like elements in *Colosteus scutellatus* with slightly expanded ends that can be interpreted as hypobranchials. Furthermore, Hook (1983, fig. 12a, b) described elongated dentigerous branchial platelets that closely resemble those of *Greererpeton*, but are proportionally longer.

3.1.6. Baphetidae. Milner & Lindsay (1998) provisionally designated a stout bone between the mandibular rami of *Baphetes* cf. *B. kirkbyi* as a ceratobranchial. However, since this bone is comparatively short and straight, this interpretation is doubtful. Clack (2003) tentatively described a possible ceratohyal in *Kyrinion martilli*. The bone has a slightly expanded proximal end, a short shaft and a blade-like expanded distal portion. Apart from articulatory facets at the distal and proximal ends, a further facet is present at the mid length of the bone.

3.2. Temnospondyli

3.2.1. Dvinosauria: *Dvinosaurus*. The basibranchial of *D. primus* is preserved in one specimen, PIN Am/40, and only its anterior part is exposed. It is a robust, rod-like bone and rounded-oval in cross section (Fig. 3a). The slightly expanded anterior portion is straight and becomes deeper than the shaft. In the same specimen, the first pair of hypobranchials is almost one third longer than the second pair (Fig. 3a). The first hypobranchials appear to be broader distally than proximally. Two pairs of ossified hypobranchials are preserved in the smaller skull of *D. primus* (PIN 2005/39). The first pair is slightly longer than the second pair (Fig. 3b). The bones are robust, round to ovate in cross section and slightly expanded at the ends. One pair of hypohyals is present in PIN Am/41,

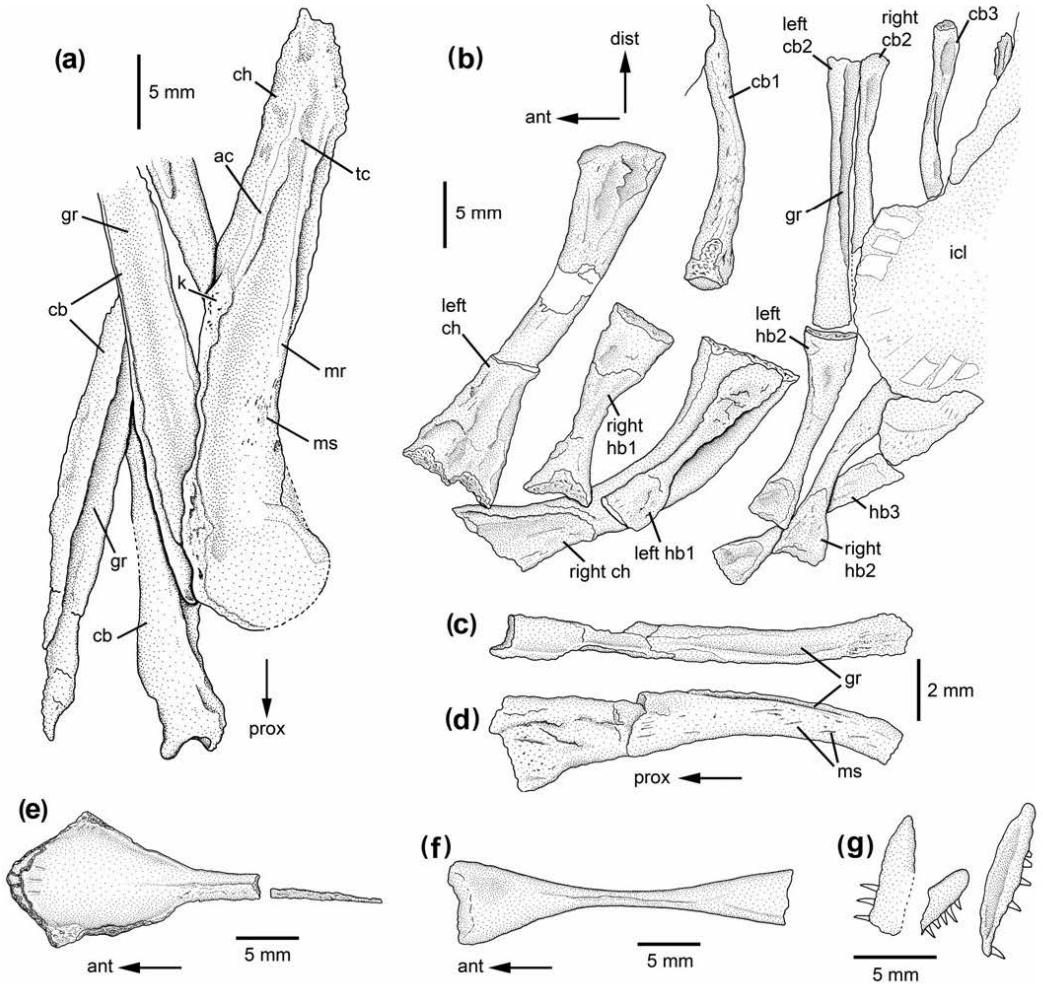

Figure 2 Hyobranchial skeleton of stem-tetrapods: (a) *Acanthostega gunnari* MGUH f.n.1227, ceratohyal and ceratobranchials; (b) *Adelogyrinus simorhynchus* NMS.G.1889.101.17, hyobranchial skeleton and anterior part of interclavicle; (c d) *Adelospondylus watsoni* NMS.G.1885.57.51, isolated ceratobranchial: (c) posterolateral view; (d) anterior view; (e g) *Greererpeton burkemorani*: (e) CMNH 11090, basibranchial in ventral view; (f) CMNH 11130, basibranchial in ventral view; (g) CMNH 11219, dentigerous branchial platelets. Abbreviations: ac = anterodorsal crest; ant = anterior; cb = ceratobranchial; ch = ceratohyal; dist = distal; gr = groove; hb = hypobranchial; icl = interclavicle; k = knob; mr = medial ridge; ms = muscle scars; prox = proximal; tc = transversally aligned crest.

the right one being well preserved (Fig. 3a) and reaching about half the length of the first hypobranchial. It is rounded and rhombic in outline, with the medial portion being bulge-like, thickened and medially concave, whereas the lateral portion is thinner and laterally convex. Both portions are separated by a slight longitudinal depression.

The ossified part of the right ceratohyal is well preserved in lateral and dorsal view in PIN 2005/39, whereas the left element has been removed since the descriptions of Sushkin (1936) and Bystrow (1938). It is a broad, stout bone with expanded proximal and distal ends (Fig. 3c). Its distal end is blade-like, rounded and laterally concave; this is the broadest part of the element. The concavity narrows and extends towards the proximal end. It is framed anterodorsally by a strong, bulge-like thickening, whereas the posteroventral margin is thinner. The distal end of the bulge-like thickening forms a lateral process (*tuberculum ceratohyalis sensu* Bystrow 1938 and Shishkin 1973) with unfinished surface. From the base of this process, a thinner process extends anterodorsally and forms the anterior edge of the posterior blade; dorsally (distally), it forms an elongate, unfinished surface.

The description of the four pairs of ceratobranchials by Sushkin (1936) and Bystrow (1938) was based on the skull PIN 2005/39. Since then, the left ceratobranchials have been removed, and the right ceratobranchials are in a very poor state of preservation. It is clearly evident that ceratobranchial 1 is the most robust branchial arch, but it cannot be determined if two grooves are present on it, as stated by Bystrow (1938). In

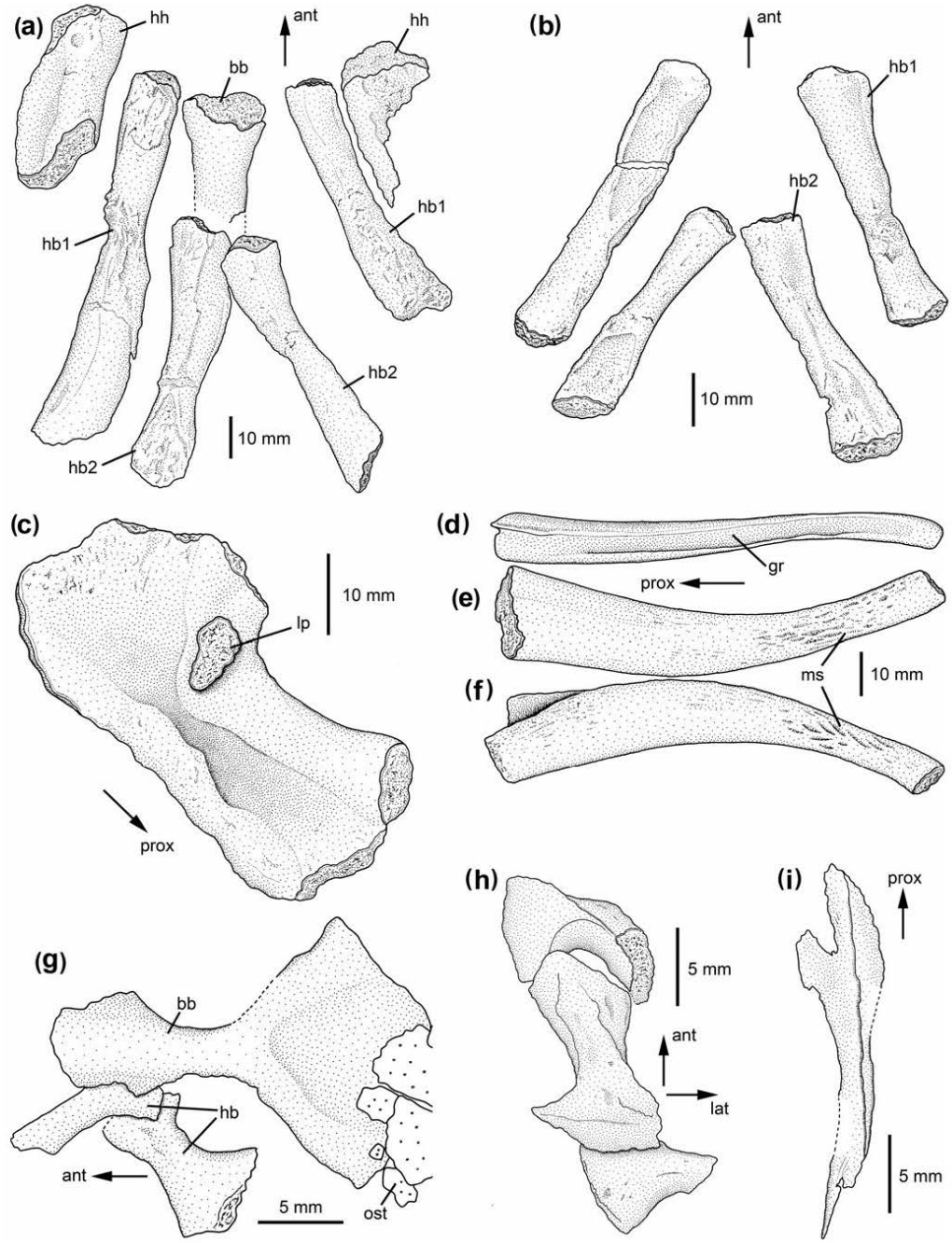

Figure 3 Hyobranchial skeleton of dvinosaurian temnospondyls: (a–c) *Dvinosaurus primus*: (a) PIN Am/40, basibranchial, hypobranchials and hypohyals in ventral view; (b) PIN 2005/39, hypobranchials in ventral view; (c) PIN 2005/39, ceratohyal in lateral view; (d–f) *Dvinosaurus campbelli*, PIN 4818/410, isolated ceratobranchial: (d) posterolateral view; (e) posterior view; (f) anterior view; (g–i) *Trimerorhachis insignis*: (g) UCMP 105146, basibranchial and two right hypobranchials in ventral view; (h) UCMP 105175, three left hypobranchials in ventral view; (i) UCMP 105221, ceratohyal. Abbreviations: ant = anterior; bb = basibranchial; gr = groove; hb = hypobranchial; hh = hypohyal; lat = lateral; lp = lateral process; ms = muscle scars; ost = osteoderm; prox = proximal.

PIN Am/41, three ceratobranchials are located on the left and at least two on the right side behind the skull, but they are very poorly preserved. The following description is based on well-preserved, isolated ceratobranchials of *D. campbelli* (mainly PIN 4818/410). The ceratobranchials are robust, curved elements that are well ossified (Fig. 3d–f). The proximal half is broad and anteroposteriorly flattened. The element tapers continuously towards its distal tip, with the proximal end attaining almost three times the width of the distal end. The posterolateral groove for the branchial artery (Sushkin 1936; Bystrow 1938; Schoch & Witzmann 2011) is clearly visible (Fig. 3d), but appears proportionally shallower and narrower than that of *Acanthostega*. The groove becomes shallower distally and disappears before reaching the distal tip. Proximally, the groove expands into a broad depression. The distal third of the anterior and posterior face possesses distinct muscle scars consisting of ridges and depressions (Fig. 3e, f), closely resembling those of *Adelospondylus* (Fig. 2d).

3.2.2. Dvinosauria: *Trimerorhachis*. The basibranchial of *Trimerorhachis insignis* consists of a stout, short shaft and is broadened anteriorly and posteriorly (Fig. 3g). The ventral surface of the anterior broadening is convex and becomes slightly concave towards the lateral ends where the bone gets thinner. The shaft is dorsoventrally flattened in cross-section and bears no ventral crest. The posterior part of the basibranchial is extremely expanded, forming a triangular blade which is approximately double the width of the anterior broadening. The ventral surface of the posterior blade is concave. The posterior expansion is almost half the length of the complete basibranchial and is dorsoventrally thinner than the anterior portion. The basibranchial is not bent in a ventral or dorsal direction.

Three pairs of short hypobranchials are present, whose morphology is best visible in UCMP 105146 and 105175 (Fig. 3g, h). The anterior two pairs have hook-like proximal and distal expansions, and the third pair is smaller and only proximally broadened.

In UCMP 105221 is an ossified element that is approximately the same length as the basibranchial and is located anterior to the ceratobranchials. The bone is flattened, rod-like, slightly bent, and is expanded proximally into a blade that is more than double the width of the shaft (Fig. 3i). The distal end appears to taper in an acute apex. A sharp crest is aligned longitudinally along shaft and blade. This bone most probably represents a ceratohyal.

Ceratobranchials in *Trimerorhachis* were described by Olson (1979), Witzmann (2004) and Schoch & Witzmann (2011). Olson (1979) suspected five pairs of ceratobranchials in *Trimerorhachis*, whereas Boy & Sues (2000) regarded the first ceratobranchial in Olson's (1979, fig. 7) figure as a ceratohyal. According to Witzmann (2004) and Schoch & Witzmann (2011), four pairs of ceratobranchials are present, each of which is a slender, slightly curved element with widened proximal end. A posterolateral groove runs from the proximal to the distal end. The grooves are broad, proportionally comparable to those of *Acanthostega*, but they are not as deep. Branchial platelets with three or four teeth at the posterior edge have been found associated with the ceratobranchials (Witzmann 2004).

3.2.3. Dvinosauria: *Thabanchuia*. The basibranchial of *Thabanchuia oomie* consists of a short, stout shaft and is anteriorly and posteriorly distinctly expanded (Fig. 4a). The shaft is dorsoventrally flattened in cross-section and bears no ventral crest. The anterior expansion is bulge-like convex ventrally in its median part (as the anterior continuation of the shaft), but flattens increasingly in an anterior direction. It becomes dorsoventrally thinner laterally where it has a ventrally concave surface. The posterior expansion is dorsoventrally thinner with respect to the shaft, faintly concave ventrally and has a bifurcated posterior end with two small, blunt processes. The basibranchial is neither curved dorsally nor ventrally.

At least three pairs of slender, slightly curved ceratobranchials are present (Fig. 4b). As stated by Warren (1999), the ceratobranchials appear hollow inside, indicating perichondral ossification of the elements, whereas the inner parts were still cartilaginous. They are somewhat expanded proximally and may possess a slightly bifurcated proximal end, reminiscent of the ceratobranchials of *Acanthostega*. Posterolateral grooves extend almost the entire length of the ceratobranchials, but diminish in depth proximally and distally.

The ascending process of the clavicle is clearly visible in UCMP 42781 and 42780. This process bears a broad lamina which extends medially and is anteriorly concave (Fig. 4c). This lamina can be interpreted as a postbranchial lamina.

3.2.4. Dvinosauria: *Isodectes*. In one specimen of *Isodectes obtusus* (AMNH 11037), the basibranchial is preserved as a slender, rod-like element with a ventrally concave anterior expansion that is framed by elevated lateral margins (Fig. 4d). A sagittal crest divides the anterior expansion into two equally sized areas. The basibranchial gets conspicuously deeper towards the shaft, where it is much deeper than wide and tapers ventrally to a thin, sharp crest. The posterior portion widens again and attains two thirds of the width of the anterior portion.

The dentigerous branchial platelets that were attached to the cartilaginous ceratobranchials in life are quadrangular, or only slightly longer than wide (Fig. 4e). One edge is bulge-like thickened and bears 5–6 teeth. Because of incomplete preservation, it cannot be ascertained how many rows of branchial platelets were present in *Isodectes*. Milner (1982) described a small larva of *Isodectes* with a rod-like basibranchial that has faintly expanded anterior and posterior ends, dentigerous branchial platelets and three pairs of external gills.

3.2.5. Further dvinosaurians. *Kourerpeton bradyi* is represented by a single specimen for which locality and geological age are unknown. It has four pairs of ceratobranchials preserved (Olson & Lammers 1976, fig. 1). A revision of this taxon is currently being undertaken by Marcello Ruta and Andrew R. Milner. Berman (1973) described the only known specimen of *Lafonius lehmani*, which might be a larval or juvenile specimen. From the hyobranchial apparatus, Berman (1973) identified elongate dentigerous branchial platelets with space for approximately ten teeth at one margin (Berman 1973, fig. 5e).

3.2.6. Zatracheidae: *Acanthostomatops*. Three or four pairs of ossified curved ceratobranchials are present in larval *Acanthostomatops vorax* that lack grooves and branchial teeth (Steen 1937; Witzmann & Schoch 2006). A basibranchial and hypobranchials have not been found. In an adult specimen, Witzmann & Schoch (2006) noted the absence of ossified ceratobranchials; instead, they identified at least four pairs of slender, linear bones ventral to the basal plate of the parasphenoid and interpreted them as part of a tongue supporting the hyobranchium.

3.2.7. Dissorophoidea: Micromelerpetontidae. From the larval hyobranchial apparatus of *Micromelerpeton credneri*, branchial platelets that are rounded rectangular and have up to six teeth are preserved (Boy 1995). The platelets are strongly concave on the internal side that was attached to the four pairs of cartilaginous ceratobranchials. In a few individuals, two pairs of feebly ossified hypobranchials and ceratohyals (?hypohyals), but no basibranchials, are preserved (Boy 1995, 2003; Boy & Sues 2000). The hyobranchium of the adult, land-dwelling individuals is not known (Boy 1995).

In contrast to *Micromelerpeton*, *Branchierpeton amblystomum* is known only from larval specimens. The basibranchial is a tiny rod-like element which is anteriorly and posteriorly slightly

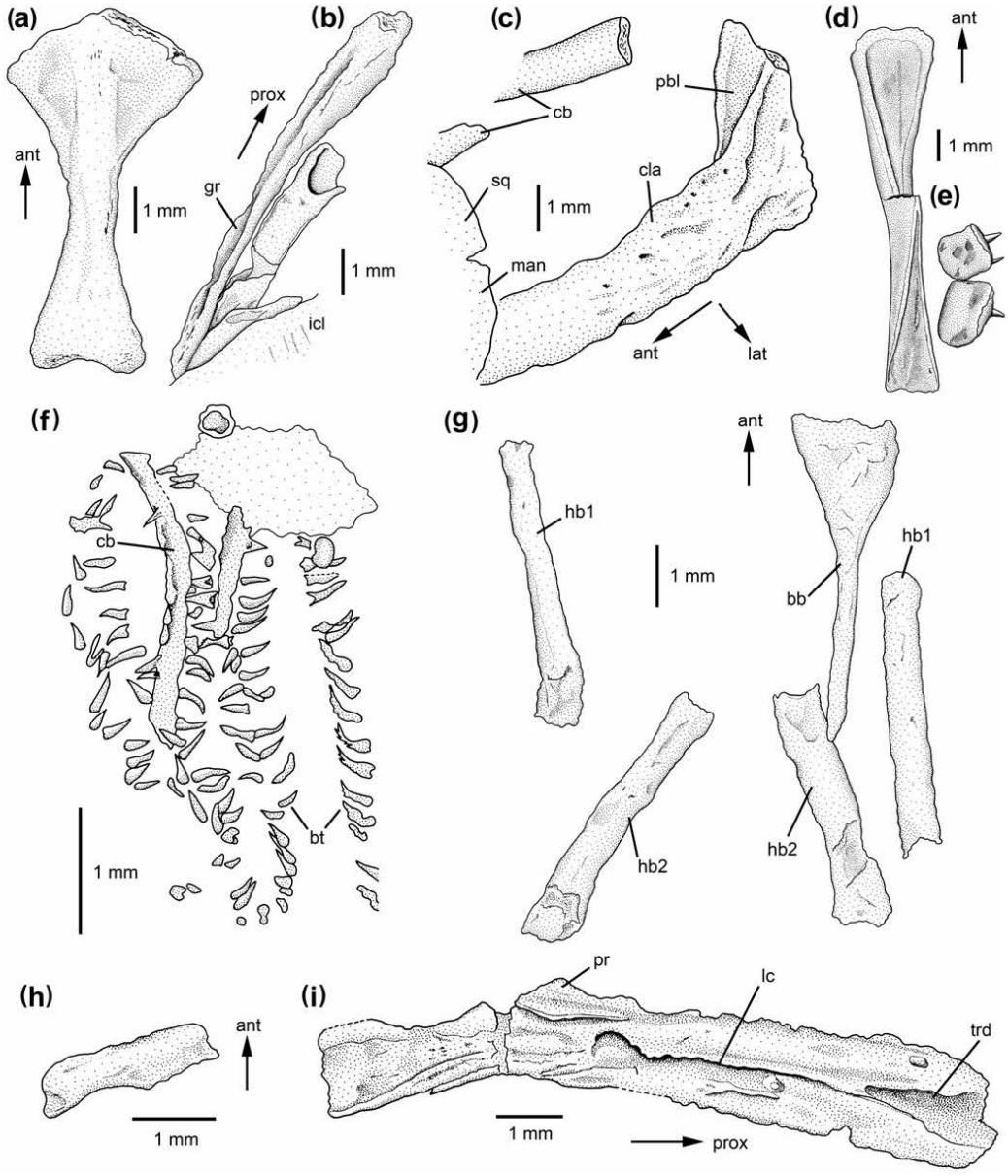

Figure 4 Hyobranchial skeleton of dvinosaurian and dissorophoid temnospondyls: (a c) *Thabanchula oomie*: (a) UCMP 42780 (holotype), basibranchial in ventral view; (b) UCMP 42781, ceratobranchials; (c) UCMP 42780 (holotype), clavicle in anterolateral view showing postbranchial lamina; (d e) *Isodectes obtusus*, AMNH 11037: (d) basibranchial in ventral view; (e) dentigerous branchial platelets; (f) *Apateon gracilis*, MB.Am.406, ossified ceratobranchials with branchial teeth; (g h) *Micropholis stowi*: (g) BSM 1934 VIII 43 (specimen B *sensu* Broili & Schröder, 1937), basibranchial and hypobranchials in ventral view; (h) BSM 1934 VIII 43 (specimen A *sensu* Broili & Schröder, 1937), ceratohyal; (i) *Platyrhinops lyelli*, MB.Am.23, ceratohyal of a large individual. Abbreviations: ant = anterior; bb = basibranchial; bt = branchial teeth; cb = ceratobranchial; cla = clavicle; gr = groove; hb = hypobranchial; icl = interclavicle; lat = lateral; lc = longitudinal crest; man = mandible; pbl = postbranchial lamina; pr = process; prox = proximal; sq = squamosal; trd = triangular depression.

expanded (Werneburg 1991, fig. 13d; pers. obs. MMG SaP179). The morphology of the branchial platelets corresponds to those of *Micromelerpeton*. One specimen of *Branchierpeton* (MNC-F 10368) has four pairs of ossified ceratobranchials preserved (described by Werneburg 1998 as a larval *Acanthostomatops vorax*, but see assignment to *B. amblystomum* in Witzmann & Schoch 2006). The ceratobranchials are long, slender elements whose proximal ends are expanded (approximately twice the width of the shaft), whereas the distal ends are tapering and hook-like. The original bone surface is not preserved, but in places, the denser perichondral bone (i.e. the cortex) can be distinguished from the spongy endochondral bone.

3.2.8. Dissorophoidea: Branchiosauridae and Trematopidae. Branchiosaurids have a highly derived larval hyobranchial apparatus adapted to filter feeding on planktonic prey (Boy & Sues 2000; Schoch & Milner 2008). The often multi-ended branchial teeth are not associated with bony platelets, but are isolated and directly attached to the four pairs of (mostly) cartilaginous ceratobranchials. Six rows of teeth are present and face towards each other, forming a zipper-like structure in the three pairs of gill clefts (Boy & Sues 2000). Ossified elements of the branchiosaurid hyobranchium comprise a tiny, rod-like basibranchial, hypobranchials and ceratohyals (or hypohyals), similar to those of micromelerpetontids (see above) (Werneburg 1991; Boy & Sues 2000). Few specimens of branchiosaurids with ossified ceratobranchials are known (Werneburg 1991). In the specimen of *Apateon gracilis* (MB.Am.406), the slightly curved ceratobranchials are long, slender and not expanded at their ends (Fig. 4f). The larvae of trematopids also have a hyobranchial apparatus that closely resembles that of branchiosaurids and was adapted for filter feeding (Milner 2007; Schoch 2009). The hyobranchium of metamorphosed branchiosaurids and trematopids is unknown.

3.2.9. Dissorophoidea: Amphibamidae. The basibranchial of *Micropholis stowi* is clearly evident in ventral exposure in individual B of specimen BSM 1934 VIII 43 (*sensu* Broili & Schröder 1937). It consists of a deep, narrow shaft that shows no posterior expansion, whereas the anterior portion is conspicuously expanded and attains more than five times the width of the shaft (Fig. 4g). The ventral surface of the anterior broadening is smooth. The basibranchial shows no ventral or dorsal curvature. Two pairs of robust hypobranchials are visible in individual B. They are about twice as broad as the basibranchial shaft and roundish in cross-section, and attain about 90% the length of the basibranchial. An ossified, short element anterolateral to the basibranchial fragment in individual A was interpreted as a hypohyal or a ceratohyal by Boy (1985). In the present study, this rod-like bone is interpreted as ossified part of a ceratohyal due to its elongate shape (Fig. 4h).

Pasawioops mayi has a very slender basibranchial whose anterior end is expanded and flattened (Fröbisch & Reisz 2008). These authors further described one pair of hypobranchials, which are rod-like elements and are longer and more robust than the basibranchial.

Sigurdsen & Bolt (2010, fig. 3b) reported feebly ossified, slender hyobranchial elements in a few specimens of *Doleserpeton annectens*. They consist of a short basibranchial bone ("basihyal") and a pair of rod-like ceratohyals and one hypobranchial.

Clack & Milner (2010) detected an elongated, flattened bone in the anterior region of the palate of a small and a larger specimen of *Platyrhinops lyelli* and interpreted the bones as ceratohyals. The small specimen (MB.Am.331) bears two rod-like bones ventral to the vomers. As Clack & Milner (2010) pointed out, it cannot be decided if the two elements represented one element that is broken, or two separate bones. The bones are slender and show no differentiation, except for the fact that the anatomical right element bears a wide longitudinal groove all along its length. In the larger specimen (MB.Am.23), the element found by Clack & Milner (2010) is broader and flattened and is slightly curved (Fig. 4i). It bears a longitudinal, sharp crest on its (presumed) ventrolateral side, dividing the surface into equal dorsal and ventral parts. At the (presumed) proximal portion, the crest is divided and frames a notch-like, triangular depression. In the (presumed) distal third of the bone, the medial crest has diminished. There is a pointed elevation or process in the distal third of the (presumed) anterior margin. At least the bone in the larger skull (MB.Am.23) can be interpreted as ceratohyal with some confidence, because of the flattened, albeit slender morphology and its anterolateral location ventral to the skull.

Bourget & Anderson (2011) detected a pair of poorly preserved, flattened elements in *Rubeostratilia texensis* that resemble the described possible ceratohyal in the small specimen of *Platyrhinops*. However, their orientation and location ventral to the parasphenoid might indicate that they represent hypobranchials.

3.2.10. Eryopidae: *Onchiodon*. In larvae of *Onchiodon labyrinthicus*, Boy (1990) and Witzmann (2005) described the rod-like basibranchial that has flattened anterior and posterior ends. The anterior end is more expanded than the posterior one. The basibranchial is unknown in adult *O. labyrinthicus* and *O. thuringiensis* (see Werneburg 2007), but Werneburg (1997, figs 1d, 4b) described and illustrated the basibranchial in adult specimens of *O. frossardi*. In this form, the expanded anterior end of the basibranchial has approximately four times the width of the rather short shaft, and the posterior end attains almost the width of the anterior end. There is no evidence of downwards curvature of the anterior portion of the bone. The dentigerous branchial platelets of *Onchiodon* larvae correspond in morphology and arrangement to those of micromelerpetontids (Boy 1990). Four pairs of slender ceratobranchials without grooves are ossified in a number of specimens of *O. labyrinthicus*, consisting of spongy bone, to which the branchial platelets are attached (Witzmann 2005).

3.2.11. Temnospondyli *incertae sedis*: *Iberospondylus*. The basibranchial of *Iberospondylus schultzei* (PU-ANF 14) is a robust, rod like element with a distinctly expanded, flattened anterior end (Fig. 5a, b). This anterior portion is curved ventrally and has two concave areas on its ventral surface, separated in the midline by a shallow longitudinal crest. The slender shaft is deeper than wide in cross section. The posterior end is flattened again and is expanded, but attains less than half the width of the anterior portion.

3.2.12. Stereospondylomorpha: *Sclerocephalus*. The ontogeny of the basibranchial in *Sclerocephalus haeuseri* was described by Boy (1972, 1974, 1988) and Schoch (2003), highlighting the proportional broadening of the anterior end during growth. In adult specimens, the basibranchial morphology resembles closely that of *Iberospondylus*, as described above (Fig. 5c, d). The ventral curvature of the expanded anterior portion and the two concave areas, however, are not apparent in larvae and juveniles. The only known specimen of *S. nobilis* (NHMM-PW 2005/2) has a large and massive basibranchial element (Fig. 5e). Its anterior expansion is further ossified anteriorly; thus, the ventral curvature is more pronounced and the bone has a shovel-like appearance. The shaft is stout and ventrally convex, and bears a sharp crest more posteriorly. Interestingly, the flattened and slightly expanded posterior portion of the basibranchial has an unfinished surface not only at its posterior edge, but at least also on the complete ventral surface (the lateral and dorsal sides are concealed). Apart from *S. nobilis*, this structure is also evident in specimen BSM AS I 575 of *S. haeuseri*.

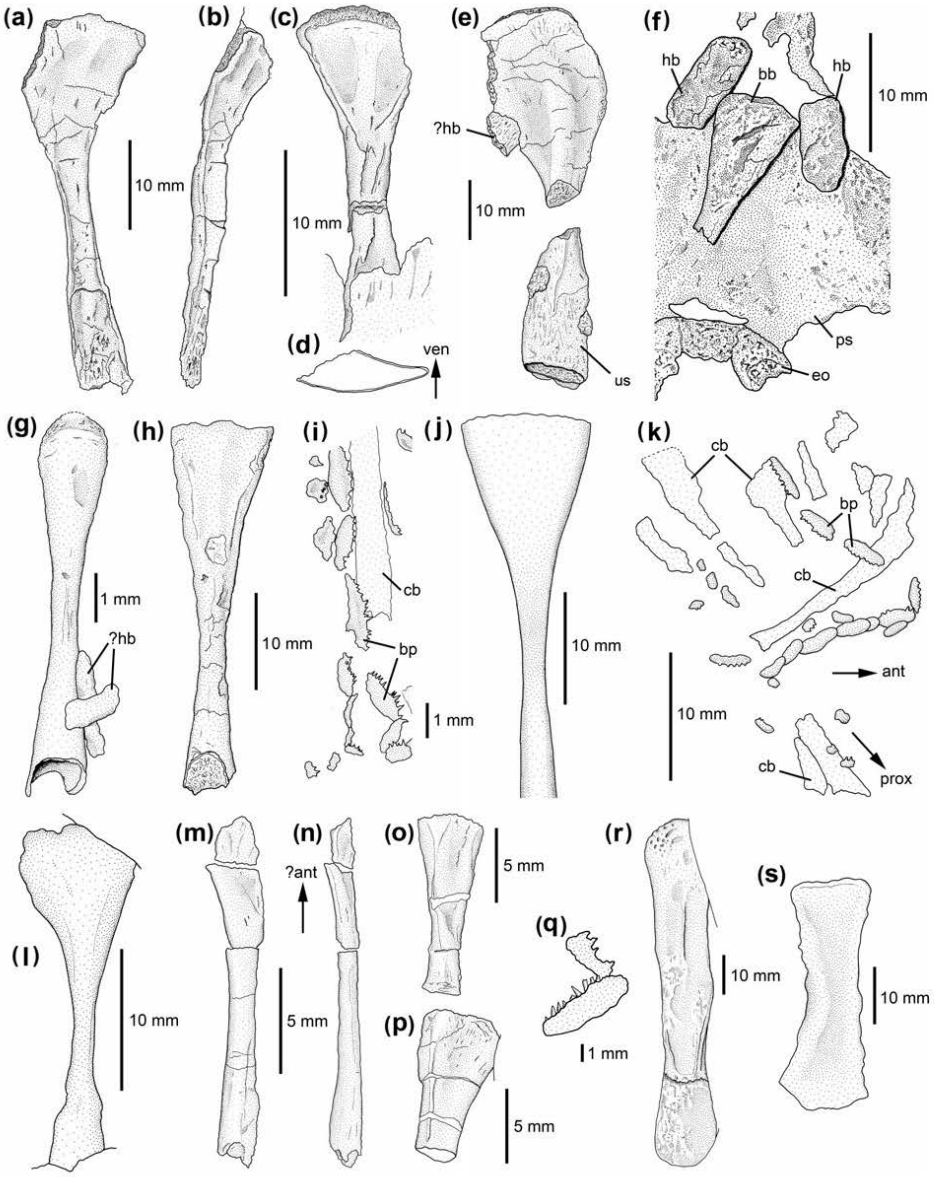

Figure 5 Hyobranchial skeleton of *Iberospondylus* and stereospondylomorph temnospondyls: (a b) *Iberospondylus schultzei*, PU-ANF 14: (a) basibranchial in ventral view; (b) basibranchial in ventrolateral view; (c) *Sclerocephalus haeuseri*, SMNS 81791, basibranchial in ventral view; (d) cross-section of the anterior portion in (c); (e) *Sclerocephalus nobilis*, NHMM-PW 2005/2, basibranchial with possible hypobranchial fragment in ventral view; (f) *Sclerocephalus haeuseri*, UHC-P 0489, parasphenoid with exoccipitals, basibranchial and hypobranchials in ventral view; (g) *Glanochthon latirostris*, MB.Am.211, basibranchial with possible hypobranchial fragments in ventral view; (h) *Glanochthon angusta*, GPIT Am 34, basibranchial in ventral view; (i) *Glanochthon latirostris*, MB.Am.224, imprint of cartilaginous ceratobranchial with ossified dentigerous branchial platelets; (j k) *Archegosaurus decheni*: (j) MB.Am.953, basibranchial in ventral view; (k) IGS U II 1/2, imprints of cartilaginous ceratobranchials with ossified dentigerous branchial platelets; (l) *Lydekkerina huxleyi*, BSM 1934 VII 44, basibranchial in ?ventral view; (m p) *Trematolestes hagdorni*, SMNS 81790: (m) basibranchial in ventral view; (n) basibranchial in lateral view; (o p) possible hypobranchials; (q) *Callistomordax kugleri*, SMNS 90700, dentigerous branchial platelets; (r) *Metoposaurus diagnosticus* SMNS 5143, basibranchial in ventral view; (s) *Stanocephalosaurus birdi* (*Wellesaurus peabodyi*), UCMP 36040, basibranchial in ventral view. When not otherwise indicated, anterior is to the top. Abbreviations: ant = anterior; bb = basibranchial; bp = branchial platelets; cb = ceratobranchial; eo = exoccipital; hb = hypobranchial; prox = proximal; ps = parasphenoid; us = unfinished surface.

In one specimen of *S. haeuseri* (UHC-P 0489), one pair of short, rod-like bones is preserved anterolateral to the basibranchial ventral to the base of the cultriform process (Fig. 5f). They are interpreted here as the anterior pair of hypobranchials, but might alternatively represent ossified hypohyals. In *S. nobilis*, a rod-like bone articulates with the right posterolateral edge of the expanded anterior portion of the basibranchial and might represent a part of a hypobranchial (Fig. 5e).

Larvae of *Sclerocephalus haeuseri* possess three or four rows of dentigerous branchial platelets that are more elongate than those of micromelerpetontids and bear between five and ten teeth (Boy 1988; Schoch 2003). These platelets are not confined to larval specimens, but occur also in at least some adults (Schoch & Witzmann 2009a).

3.2.13. Stereospondylomorpha: *Glanochthon*. In *Glanochthon latrirostris*, the basibranchial has not been found in adults (Boy 1993; Schoch & Witzmann 2009b), but is clearly visible in the juvenile MB.Am.211 (Fig. 5g). Its anterior portion is deeper and about 2.5 times wider than the shaft and slightly curved ventrally. The shaft is round in cross-section and bears a faint ventral ridge. The posterior portion is again deeper and expanded, attaining approximately 80% of the width of the anterior portion. Posterolateral to the basibranchial are two short, poorly ossified rods that might represent hypobranchials. The basibranchial is preserved in an adult specimen of *G. angusta* (GPIT.Am.34) and is more slender and less robust than that of *Sclerocephalus* (Fig. 5h). The anterior expansion is flattened and is about 3.5 times wider than the shaft, whereas the posterior extension attains only twice the width of the shaft. A ventral curvature is not determinable. Two anterior concave areas on the ventral surface are faintly indicated.

Four rows of dentigerous branchial platelets (sometimes associated with imprints of cartilaginous ceratobranchials) are preserved in small specimens and are retained at least in medium-sized skulls (Schoch & Witzmann 2009b). They are elongate and have space for more than 20 teeth (Fig. 5i).

3.2.14. Stereospondylomorpha: *Archegosaurus*. The ontogeny of the basibranchial in *Archegosaurus decheni* was documented by Hofker (1926) and Witzmann (2006) and resembles that of *Sclerocephalus*. In adults, the expanded anterior portion is six times wider than the slender shaft and is curved ventrally (Fig. 5j). The posterior portion is only slightly expanded (1.6 times the width of the shaft), but has become conspicuously deeper.

The imprints of cartilaginous ceratobranchials have distally and proximally expanded ends (Fig. 5k). Imprints of two short rod-like bones posterior to the parasphenoid might represent hypobranchials 1 and 2, and a short element anterolateral to them might be a ceratohyal (Hofker 1926, fig. 8). The morphology of the denticulate branchial platelets and their arrangement correspond to those of *Glanochthon* and are present in larvae and retained at least in middle-sized specimens. Some of the platelets may bear an ornamentation of concentric rings which may represent growth rings (Witzmann 2006).

3.2.15. Stereospondylomorpha: basal stereospondyls. Van Hoepen (1915) and Schoch (2002) described elongate branchial platelets in *Uranocentrodon senekalensis* that were arranged in at least three rows. Each platelet has space for more than 12 teeth. A rod-like bone that is located next to the cultriform process of the parasphenoid in *Lydekkerina huxleyi* (BSM 1934 VIII 44) has an anterior expanded portion that attains more than five times the width of the slender shaft (Fig. 5l). The surface of the anterior expanded portion is slightly convex. Posteriorly, the bone widens again and attains three times the width of the shaft. Because of its location and morphology, the element can be interpreted as the basibranchial.

3.2.16. Stereospondylomorpha: Lapillopsidae. Among this presumably semi-terrestrial group of stereospondyls, a specimen of *Lapillopsis nana* is preserved with a slender, rod-like bone ventral to the parasphenoid (Yates 1999, fig. 7). Yates (1999) suggested that it might represent a part of the hyobranchium and could be a possible hypobranchial (probably because of its oblique orientation with respect to the longitudinal axis of the skull). However, due to its isolated nature ventral to the parasphenoid, it might also represent a slightly rotated basibranchial.

3.2.17. Stereospondylomorpha: Trematosauroidea. In the type specimen of *Trematolestes hagdorni* (SMNS 81790), a long, very slender bone is located approximately in the midline of the skull between the orbits (Fig. 5m, n). Its shaft is round-ovate in cross-section and the caudally oriented end is flattened and slightly expanded with a concave surface. The opposite end is less expanded, and has become deeper rather than flattened. Because of its morphology and position, Schoch (2006) regarded this element as the basibranchial, and this interpretation is followed here. The element has probably rotated around 180° and the broader portion represents the anterior end. Posterior to the basibranchial is a pair of short bones (Fig. 5o, p). Because of their position and length, these bones might be hypobranchials. More posterior, lateral to the left clavicle, is a bone fragment that might represent the expanded proximal end of a ceratobranchial.

In the stem-metoposaurid *Callistomordax kugleri*, several long-ovate branchial platelets with space for approximately 15 teeth at one edge are preserved (Fig. 5q). Additionally, a slightly curved bone fragment with a longitudinal groove is present that probably represents a part of a ceratobranchial.

In specimen SMNS 5143 of *Metoposaurus diagnosticus*, a rod-like bone is preserved ventral to the cultriform process (Fig. 5r). Its shaft is stout, dorsoventrally flattened, and the anterior and posterior ends are slightly broadened and rounded. The anterior end is somewhat deeper than the shaft and bears a pitted surface. A longitudinal crest is visible in the anterior half of the bone. In the posterior half, two crests converge towards the posterior end. Morphology and location of the bone strongly suggest the interpretation as a basibranchial.

3.2.18. Stereospondylomorpha: Capitosauroidea. In two specimens of *Stanocephalosaurus birdi* (*Wellesaurus peabodyi*; UCMP 56098, 36040), a stout linear bone is visible that is located next to the cultriform process of the parasphenoid and oriented parallel to it. It is rather undifferentiated and slightly expanded anteriorly and posteriorly (Fig. 5s) and probably represents the basibranchial. Warren & Hutchinson (1988, fig. 6) described a basibranchial in *Rewanobatrachus* (*Parotosuchus*) *aliciae*. This bone has a long, slender shaft and is slightly expanded anteriorly and posteriorly. In *Parotosuchus wadei*, Damiani & Warren (1997, fig. 2) found thin rod-like bones between the clavicles and the posterior end of the mandibles. They tentatively interpreted these bones as ribs, but did not rule out the possibility that they might represent ossified ceratobranchials.

3.2.19. Stereospondylomorpha: Brachyopoidea. The small and only known specimen of the brachyopoid *Platycepsion wilkinsoni* has four ossified ceratobranchials and an ossified part of a possible ceratohyal is present anterior to them (Watson 1956; Warren & Marsicano 1998). Warren *et al.* (2011) found fragments of ossified, grooved ceratobranchials in a specimen of *Bothriceps australis*.

3.2.20. Stereospondylomorpha: *Gerrothorax* (Plagiosauridae). The view of Jenkins *et al.* (2008) is followed here that other *Gerrothorax* species cannot be differentiated from *G. pulcherrimus*. Therefore, *G. "rhaeticus"* from Sweden (Nilsson 1946) is treated here as the same taxon as *G. pulcherrimus* from Greenland (Jenkins *et al.* 2008) and Germany (Hellrung 2003). In the following, the partially articulated hyobranchial apparatus

SMNS 83866, MGUH 28919 and NRM-PZ B.18b will be described separately.

The Stuttgart specimen SMNS 83866 is an almost complete skeleton of *Gerrothorax*, in which large parts of the hyobranchial apparatus are preserved in ventral view (Fig. 6a). The large paired elements in the anterior part of the hyobranchium are elongated and rectangular in outline. The anatomical right element appears to have a concave posteromedial edge, whereas this region is obscured in the opposing element. Poor preservation precludes recognition of more anatomical details. In contrast to Hellrung (2003), who reconstructed these elements as hypohyals, they are interpreted here as the first pair of hypobranchials for the following reasons. First, the ceratobranchials and not the ceratohyals are located distal to these elements; second, comparison with tetrapodomorph fishes (Jarvik 1954, 1963; Downs *et al.* 2008), *Acanthostega* (Coates & Clack 1991; this study), other temnospondyls (Bystrow 1938; this study) and extant salamanders (e.g. Stadtmüller 1936; Deban & Wake 2000) shows the hypohyals to be mostly rather small elements proximal to the ceratohyals. If this interpretation is correct, then three ossified pairs of hypobranchialia are present in this specimen, the posterior two pairs being more slender and rod-like. Additionally, a fragment of the basibranchial can be identified between the hypobranchial elements (*contra* Hellrung 2003). It appears to be rod-like and slender. Two ceratobranchials can definitely be identified posterior to the hypobranchials (see also Hellrung 2003), and a bone fragment directly posterior to the first hypobranchial probably represents a further ceratobranchial. Thus, probably at least three ossified ceratobranchials are present in this specimen. Their following morphological description is supplemented by the isolated finds SMNS 83370 and 83382. The ceratobranchials are widened proximally in a triangular extension, and taper continuously in a distal direction (Fig. 6a–c). The shaft is slender and may be slightly curved, and broadens again somewhat at its distal end. With the exception of short striae and tiny ridges, the dorsomedial surface of the ceratobranchials is smooth. In contrast, the ventrolateral surface is rather complex. A broad, shallow ridge extends from the proximal end distally. It divides the proximal triangular expansion into two concave fields. The broad ridge increases distinctly in height at the transition from the triangular expansion to the shaft and tapers into a rather sharp ventral crest, so that the shaft becomes deeper than wide. Two grooves extend along the lateral face of the shaft, a posteroventral and an anteroventral one (Fig. 6c). The posterior of these furrows represents the distal continuation of the posterior concave field; it is rather shallow and located immediately posterior to the apex of the ridge. Anterior to the crest is a deeper furrow that represents the distal continuation of the anterior concave field. Branchial platelets and teeth are not visible. Each ceratohyal has an elongate, oval shape and is the longest preserved element of the hyobranchium. The anterolateral edge is slightly convex, whereas the posteromedial edge appears slightly concave. Approximately the proximal half of the ventrolateral surface consists of a distinct depression with longitudinal striae at the proximal end. The distal end of the element bears similar longitudinal striae, but no depression is visible.

The Copenhagen specimen MGUH 28919 is a rather small, apparently juvenile specimen from Greenland. Several ossified elements of the hyobranchium are articulated and exposed in ventral view (Fig. 6d). The large paired elements regarded as hypohyals by Jenkins *et al.* (2008) are interpreted here as hypobranchials 1 for the same reasons as the hypohyals *sensu* Hellrung (2003) in SMNS 83866 (see above). Consequently, the posterior following, much narrower element can be regarded as second hypobranchial, and the third hypobranchial is not preserved. The ventral surface of the first hypobranchial bears a ridge along the shaft and bifurcates at the distal broadening of the bone. The anterolateral edge of the bone bears a notch-like depression. If the designation as first and second pair of hypobranchials is correct, then the median, unpaired element can be interpreted as basibranchial rather than a basihyal *sensu* Jenkins *et al.* (2008). It is quite short and only slightly broader anteriorly than posteriorly. It is dorsoventrally flattened in cross-section. At least three, but probably four ceratobranchials are preserved which correspond in outline to the ceratobranchials described in the Stuttgart material. On the anatomical right side, ceratobranchial 1 is preserved only in its proximal part. Ceratobranchial 2 is straight, grooved and has a trough in its proximal end (Fig. 6d). Ceratobranchials 3 and 4 are only fragmentarily preserved, but at least ceratobranchial 3 appears to be slightly curved. On the anatomical left side, three grooved ceratobranchials are preserved (probably ceratobranchials 1–3, not shown in the Figure). Whereas the anteriormost element is rather straight, the posteriorly following ones are increasingly curved and are becoming shorter, similar to NRM-PZ B.18b (see below). The ceratohyals are the broadest elements, but in contrast to SMNS 83866, they are shorter than the ceratobranchials, probably because of incomplete ossification. They have a slightly convex lateral and a concave medial margin. The medial margin is distinctly thickened, and the proximal portion bears a notch-like depression whose length accounts for approximately one quarter of the length of the ceratohyal. In its distal part, the bone bears smaller, paired depressions.

The Stockholm specimen NRM-PZ B.18b is very poorly preserved, and only the outline of the hyobranchial elements, not their surface structure, can be seen (Fig. 6e). The first ceratobranchial is rather straight, whereas the posteriorly following three elements get increasingly curved. The length of the first ceratobranchial cannot be ascertained, but ceratobranchials 2–3 get increasingly shorter. Associated with ceratobranchials 2 and 3 are ossified branchial platelets of rectangular outline, with space for 3–4 posterior teeth (Fig. 6f). Judging from its position lateral to ceratobranchial 1, an elongate, very poorly preserved element can best be interpreted as ceratohyal (see also Nilsson 1946). The elements interpreted by Nilsson (1946) as three hypobranchials are too fragmentarily preserved to draw any conclusions.

3.2.21. Stereospondylomorpha: *Plagiosuchus* (Plagiosauridae). Next to the clavicular stem in an articulated specimen of *Plagiosuchus pustuliferus* (SMNS 84794) are several branchial platelets bearing curved teeth at one edge (Fig. 6g). Because of poor preservation, they are of ill-defined outline and it cannot be ascertained if they are quadrangular or rather elongate. Interestingly, they bear an ornament of fine, curved ridges and furrows. Four pairs of grooved ceratobranchials are ossified in *Plagiosuchus* (Schoch & Witzmann 2011, fig. 4g, h). Due to poor preservation, it cannot be determined if the ceratobranchials have the widened proximal ends that are visible in *Gerrothorax*.

3.3. Lepospondyli

3.3.1. Lysorophia. The extensive hyobranchial apparatus of lysorophians was described in detail by Wellstead (1991). Hypohyals and ceratohyals are more flattened than the rather cylindrical, stout four pairs of hypobranchials and the four pairs of ceratobranchials. Some specimens of *Brachydectes elongates* bear "accidental bones" in the first branchial arch between the hypobranchials and ceratobranchials, the homology of which is uncertain (Wellstead 1991). The ceratobranchials bear no grooves.

3.3.2. "Microsauria". "Microsaurs" are probably not a monophyletic assemblage (Marjanović & Laurin 2013, and references therein) and are therefore written in quotation

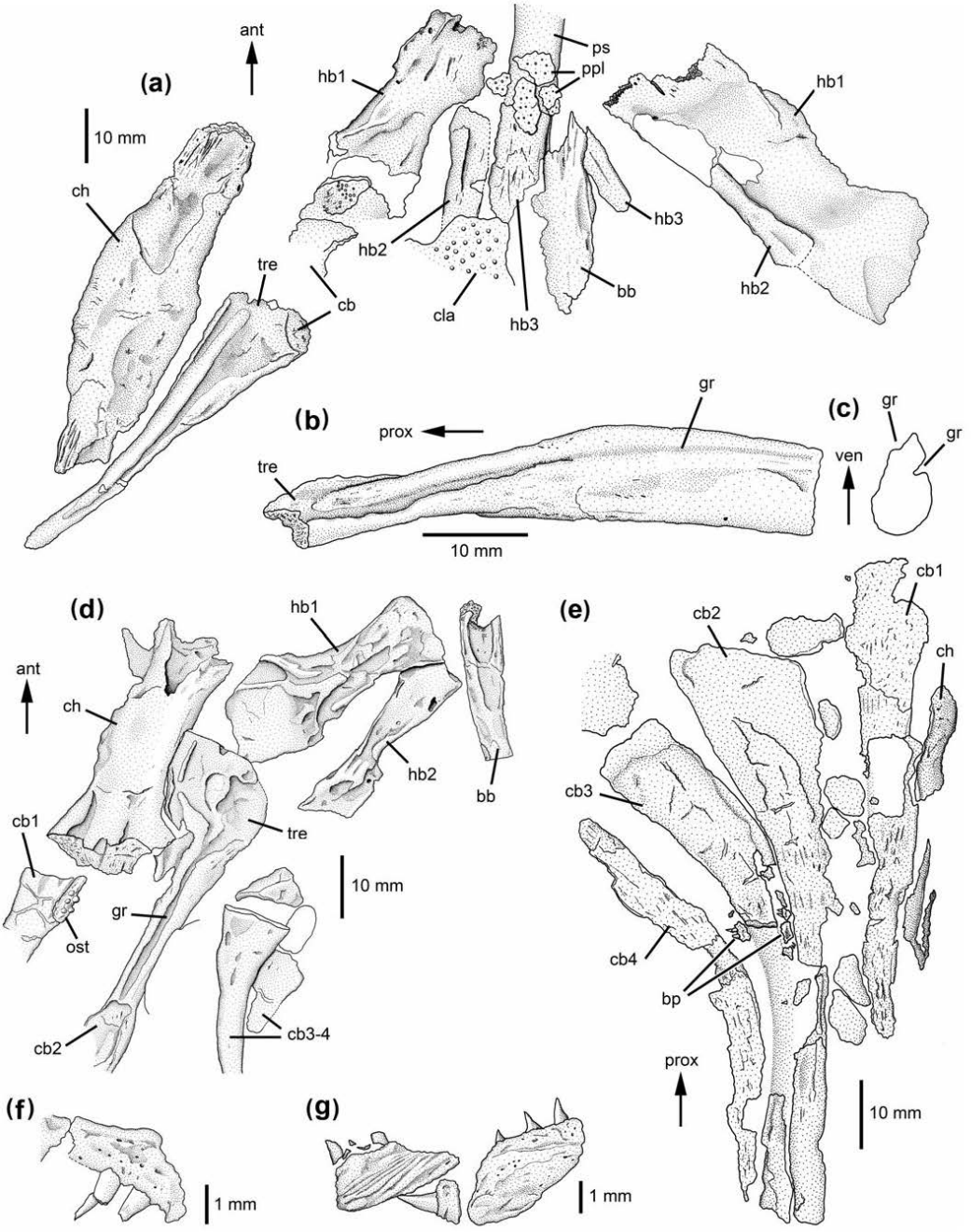

Figure 6 Hyobranchial skeleton of plagiosaurid stereospondyls: (a–f) *Gerrothorax pulcherrimus*: (a) SMNS 83866, partial hyobranchial apparatus in ventral view; (b) SMNS 83382, isolated ceratobranchial, lateral view; (c) SMNS 83382, isolated ceratobranchial, cross-section of distal end; (d) MGUH 28919: partial hyobranchial apparatus in ventral view; (e) NRM-PZ B.18, four ceratobranchials and fragmentary ceratohyal; (f) NRM-PZ B.18, dentigerous branchial platelets; (g) *Plagiosuchus pustuliferus*, SMNS 84794, dentigerous branchial platelets. Abbreviations: ant = anterior; bb = basibranchial; bp = branchial platelets; cb = ceratobranchial; ch = ceratohyal; cla = clavicle; gr = groove; hb = hypobranchial; ost = osteoderm; ppl = palatal platelets; prox = proximal; ps = parasphenoid; tre = triangular expansion; ven = ventral.

marks. *Microbrachis pelikani* is the only lepospondyl in which branchial platelets were described (Carroll & Gaskill 1978; Olori 2011). According to Olori (2011), the platelets are round or ovate and may bear three denticles. In some platelets, the bone surface is concave, probably representing the side that was attached to the ceratobranchials as in colosteids and temnospondyls (see above). In specimen AMNH 2557, posterolateral to two preserved rows of branchial platelets is a wrinkled structure that extends mediolaterally. Because of its location and alignment, this structure might represent preservation of external gills proper.

The hyobranchial apparatus of *Pantylus cordatus* is well ossified and was described by Romer (1969, fig. 16) and Carroll & Gaskill (1978) in a specimen which has been sectioned since then. Three pairs of elongate bones are present that are blade-like, expanded in their proximal portion and continue distally into a narrower stem. At about midlength, these bones curve in a dorsomedial direction. The anteriormost of these bones appears to bifurcate distally. Distal to them are located three pairs of stout, broadened bones. Because the proximal bones are proportionally very long and curved and the distal ones are rather short, the hyobranchial elements in *Pantylus* can best be designated as ceratobranchials and epibranchials *sensu* Reilly & Lauder (1988). The basibranchial or parts of the hyoid arch are not preserved.

Further microsaurs with hyobranchial remains are *Pelodosotis elongatum*, *Tambaroter carolli* and *Hapsidopareion lepton*. Narrow, rod-like hyobranchial elements of uncertain affinities (? ceratohyal and hypobranchials) are present in *Pelodosotis* and *Tambaroter* (Carroll & Gaskill 1978; Henrici *et al.* 2011), whereas in *Hapsidopareion*, a short, robust bone posterior to the articular and stapes was interpreted as a probable hyoid element by Carroll & Gaskill (1978).

3.3.3. Nectridea, Aïstopoda and Acherontiscidae. No unambiguous remains of hyobranchial elements have been demonstrated so far in nectrideans (Bossy & Milner 1998) or in aïstopods (Carroll 1998; Anderson *et al.* 2003). Carroll (1969) interpreted four disarticulated, flattened bones of rectangular outline just behind the skull of *Acherontiscus caledoniae* as elements of the hyobranchial apparatus, but a more precise assignment is not possible.

3.4. "Anthracosauria"

No cartilaginous or ossified hyobranchial skeletal elements and no branchial teeth have ever been found in the paraphyletic "anthracosaurs" (embolomeres, gephyrostegids and seymouriamorphs), despite the fact that numerous specimens of larval seymouriamorphs preserve three pairs of pinnate external gills (Ivakhnenko 1987; Klembara 1995; Bulanov 2003; pers. obs.). Pawley (2006) described a postbranchial lamina on the cleithrum of the embolomere *Archeria*.

3.5. Reconstructions of hyobranchial apparatus

The hyobranchial apparatus of different basal tetrapods are reconstructed in Figures 7 and 8 and are compared with that of the tetrapodomorph fish *Tiktaalik*. Due to the often fragmentary preservation and the poor degree of ossification, these reconstructions must in part be tentative.

4. Discussion

4.1. Phylogenetic patterns of the hyobranchium in basal tetrapods

4.1.1. Basibranchial skeleton. In osteichthyan fishes, the basibranchial skeleton might be composed of a series of cartilaginous and/or ossified basibranchial elements, or the basibranchial can be developed as a single element (Nelson 1969). The basibranchial series is most often subdivided into several ossification centres, including an anterior basihyal in actinopterygians. However, the number of elements varies between taxa, and the basal actinopterygian *Polypterus* has only a single basibranchial ossification (Fig. 1a). Among extant sarcopterygian fishes, *Latimeria* has also a single basibranchial (Fig. 1b), whereas in the extant dipnoan *Neoceratodus*, the basibranchial series comprises a basihyal and two small basibranchials. Ventral to the basibranchial series, an unpaired bone referred to as urohyal may be present in certain osteichthyans. In actinopterygians, this bone is either a tendon bone, as in *Polypterus*, or a dermal bone, as in teleosts. In sarcopterygian fishes, the element is an endoskeletal bone (Arratia & Schultze 1990).

In tetrapodomorph fishes, the basibranchial series comprises two bones, an anterior basibranchial 1 and a posterior basibranchial 2 (Jarvik 1954; Lebedev 1995; Johanson & Ahlberg 1997; Downs *et al.* 2008). Basibranchial 1 is a massive bone of octagonal shape in *Tiktaalik* (Fig. 7a), *Medoevia* and *Gogonasus*, or it is elongate rectangular as in *Eusthenopteron* and *Mandageria*. It has extensive articulation facets for the hypohyals and the first two pairs of hypobranchials. Posteriorly, the bone is connected with basibranchial 2, which is distinctly smaller and usually articulates with the third pair of hypobranchials. The vertically oriented, blade-like urohyal is connected to the ventral surface of the basibranchial series. A sublingual rod (regarded as the basihyal by Nelson 1969) may extend from basibranchial 1 towards the mandibular symphysis in *Eusthenopteron* (Jarvik 1954, 1963) and *Mandageria* (Johanson & Ahlberg 1997). It is difficult to assess to which element of the basibranchial series the single ossified basibranchial element in basal tetrapods is homologous. According to the relative position of the hypobranchials, it might represent the first basibranchial of tetrapodomorph fishes, or it could likewise represent a fusion between basibranchials 1 and 2. Bystrow (1938) regarded the basibranchial in *Dvinosaurus* as the second basibranchial, but gave no reasons for this assignment. The basibranchial skeleton in *Acanthostega* is not preserved. Given the excellent preservation of the partially articulated hyobranchium in this Devonian stem-tetrapod, one can assume that the basibranchial skeleton was cartilaginous in the living animal and is thus not preserved. The colosteid *Greererpeton* is the earliest and basalmost tetrapod in which the basibranchial is known; therefore, basibranchial morphology of this form can be regarded as the plesiomorphic state for basal tetrapods: a slender, rod-like shaft bearing a ventral crest, a broadened, flat anterior portion, and a posterior end that is broadened to a lesser degree than the anterior one. The ventral surface of the anterior broadening bears narrow concave portions next to the lateral margins. Anterior and posterior extensions in cartilage were present, and no articulation facets for hypohyals and hypobranchials are visible.

In further basal tetrapod evolution, an ossified basibranchial is only known in temnospondyls where it retained its rod-like morphology; however, some modifications are observable in different temnospondyl lineages. Within dvinosaurians, the ventral crest is absent, and the bone is rather stout with conspicuously expanded anterior and posterior ends in *Trimerorhachis* and *Thabanchuia*. In *Dvinosaurus*, in contrast, the anterior portion of the basibranchial is only slightly expanded and deeper than the shaft. This morphology might be regarded as a paedomorphic trait, since the basibranchials of larval and juvenile stereospondylomorphs (Boy 1974; Schoch 2003; Witzmann 2006; this study) have a very similar morphology. The dvinosaurian *Isodectes* has a similarly slender basibranchial, but it differs

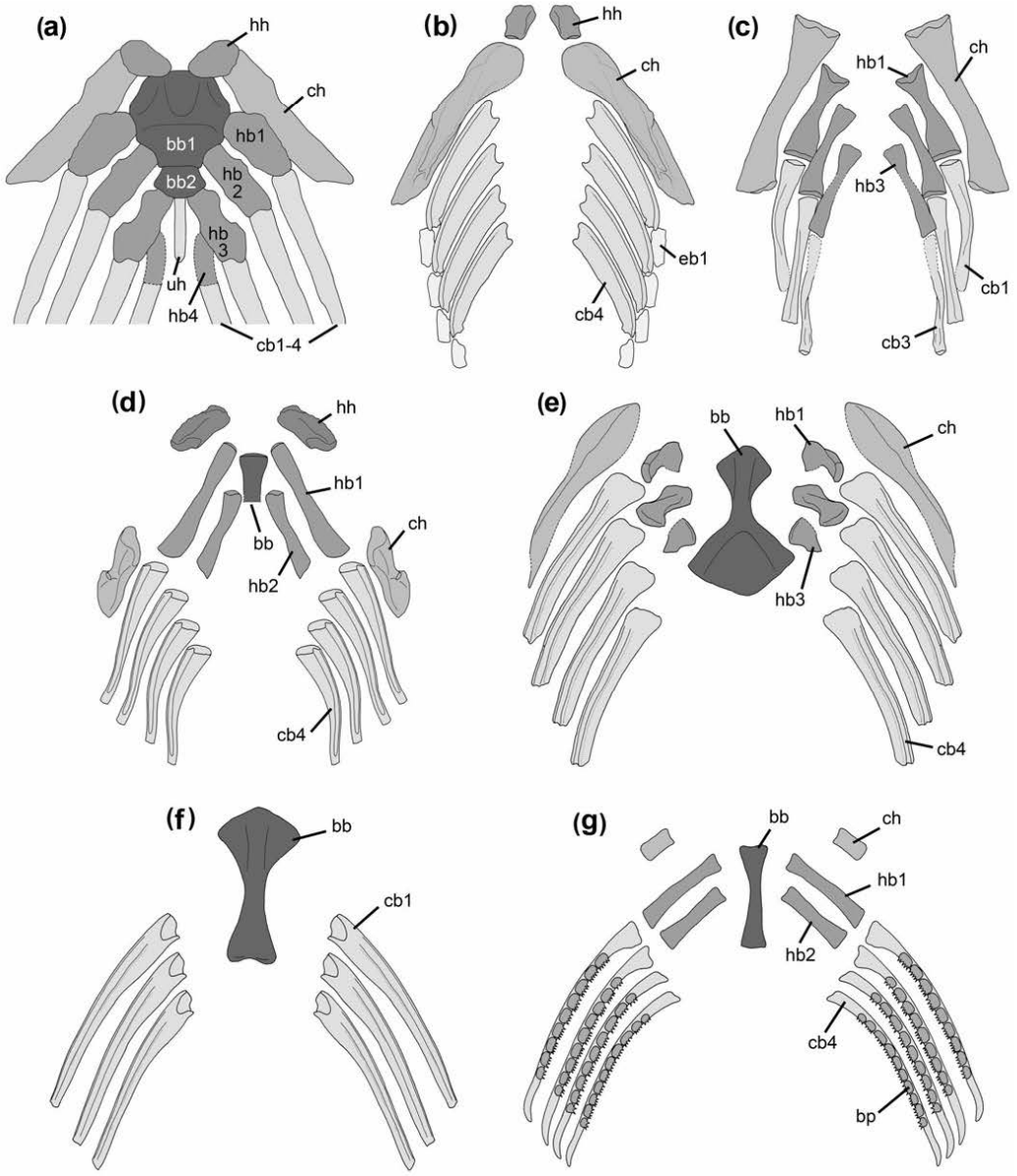

Figure 7 Reconstructions of hyobranchial apparatus in *Tiktaalik* and different basal tetrapods: (a) *Tiktaalik roseae*, redrawn after Downs *et al.* (2008); (b) *Acanthostega gunnari*, based on MGUH f.n.1227 and 1300; (c) *Adelogyrinus simorhynchus*, based on NMS.G.1889.101.17; (d) *Dvinosaurus* sp., based on PIN 2005/39 and 4818/410; (e) *Trimerorhachis insignis*, based on UCMP 105146, 105175, 105221 and 154434; (f) *Thabanchuia oomie*, based on UCMP 42780 and 42781; (g) larval micromelerpetontid, based on MNC-F 179 and MMG SaP 10368 (*Branchierpeton amblystomum*), ceratohyals and hypobranchials are supplemented after Boy & Sues (2000, *Micromelerpeton credneri*). Abbreviations: bb = basibranchial; bp = branchial platelets; cb = ceratobranchial; ch = ceratohyal; eb = epibranchial; hb = hypobranchial; hh = hypohyal; uh = urohyal.

from other dvinosaurians by a sharp ventral crest formed by the shaft and the distinct ventral concavity of the anterior broadened portion. In the amphibamid dissorophoids *Micropholis* and *Pasawioops*, the basibranchial is slender and anteriorly expanded, as in *Greererpeton*, but has no ossified posterior expansion. In basal stereospondylomorphs, the basibranchial has retained the slender outline as in colosteids, but the anterior expansion is curved ventrally, and the lateral concavities on the ventral surface of the expansion, as present in *Greererpeton*, have become two distinct concave areas. The temnospondyl *Iberospondylus*, whose phylogenetic affinities are still not clear (Schoch 2013), has exactly the same basibranchial morphology as basal stereospondylomorphs. In the basal stereospondyl *Lydekkerina*, the basibranchial is similar to that of *Micropholis*, whereas in more derived stereospondyls, the element seems to ossify rarely and is only known in *Stanocephalosaurus*, *Rewanobatrachus*, *Trematolestes* and *Metoposaurus*, where it is a rather undifferentiated rod. The fact that, from the hyobranchial apparatus, only the basibranchial was ossified in several taxa of early tetrapods might be connected with the functional role of this element as the point of insertion of the rectus cervicis muscle. This muscle aids in depression of the mandible when pulled posteroventrally in larval salamanders, a mechanism that is probably plesiomorphic for gnathostomes (Lauder & Reilly 1994). Additionally, the rigid basibranchial bone served for pressing the prey against the toothed palate to seize and to manipulate it. In particular, the elaborated, downturned anterior extension of the basibranchial in basal stereospondylomorphs may have served for the insertion of a powerful rectus cervicis muscle. In more derived stereospondylomorphs, the stereospondyls, a retroarticular process is often well developed on the mandibles and thus a strong depressor mandibulae muscle is able to insert on the lower jaw (Schoch & Milner 2000). This development in stereospondyls might be correlated with a morphological simplification (and obviously frequent non-ossification in many forms) of the basibranchial.

Although the general configuration, especially of the larval (or paedomorphic) hyobranchial apparatus of extant salamanders (Fig. 1c) and caecilians, resembles that of early tetrapods (anurans are highly derived because of the extreme feeding specialisations of their larvae, Lauder & Reilly 1994), homologisation of the basibranchial elements in extant amphibians and early tetrapods has proven to be difficult. In extant larval salamanders, the basibranchial series consists of a first basibranchial (or anterior copula) and a second basibranchial (posterior copula or urohyal), whereas adult forms have a first basibranchial that is followed posteriorly by a median bone, the os thyroideum (Rose 2003). A basibranchial series of basihyal and posteriorly following basibranchials 1–4 were described in larvae of the caecilian *Epicrionops bicolor* (Wake 1989), whereas in the adult form, only one basibranchial is present (the reformed basibranchial 1). At present, it cannot be said which of the basibranchial elements in salamanders and caecilians corresponds to the basibranchial ossification in basal tetrapods. There might have been two or more basibranchials elements in early tetrapods, from which only one element was ossified and is preserved; alternatively, the single preserved basibranchial element might have given rise to the two or more centres, as in extant amphibians. Boy (1974) suspected that the two basibranchial elements in larval urodeles are homologous to the single basibranchial bone in basal tetrapods, whereas Jarvik (1954, 1963) and Kanyukin (2006) homologised basibranchial 2 in larval urodeles with the urohyal of tetrapodomorph fishes.

4.1.2. Hyoid arch. The hyoid arch in basal tetrapods is represented by hypohyals and ceratohyals, whereas the hyomandibula was modified into the stapes in stem-tetrapods (Clack 1992). Where preserved in tetrapodomorph fishes, the small hypohyals are stout, curved elements that fit into articulation facets on the anterodorsal edge of basibranchial 1 (Jarvik 1954; Johanson & Ahlberg 1997; Long *et al.* 1997; Downs *et al.* 2008) (Fig. 7a). In basal tetrapods, these elements are very rarely preserved, but the known hypohyals of basal tetrapods remain stout and rather small, and are not received by ossified facets on the basibranchial (Fig. 7b, d). Whereas the ceratohyals of *Medoevia* and *Eusthenopteron* consist of an anterior (ceratohyal 2) and posterior (ceratohyal 1) part (Jarvik 1954; Lebedev 1995), the proportions of the ceratohyal in basal tetrapods resemble those of the tetrapodomorph fish *Tiktaalik* (Downs *et al.* 2008, fig. 6, supplementary fig. 3). In *Tiktaalik*, the ceratohyal is a single element that is elongate, blade-like, tapering distally, and has its widest portion in its proximal half (Fig. 7a). The proximal end forms an articulation surface with the hypohyals. In basal tetrapods, the ceratohyal is adequately preserved only in rare cases. When fully ossified, it is the longest element of the hyobranchial apparatus, as in *Acanthostega* (Fig. 7b), adelogyrinids (Fig. 7c), *Trimerorhachis* (Fig. 7e) and *Gerrothorax* (Fig. 8d), and appears broader and more flattened than the other paired elements. In *Dvinosaurus* (Fig. 7d) and the baphetid *Kyrinion* (Clack 2003), the blade-like ceratohyals are proportionally much stouter elements. This can probably be attributed to incomplete ossification of the element, i.e. the distal and proximal portions were cartilaginous and only the middle part of the shaft was ossified. The amphibamid *Platyrhinops* has a long and slender, albeit flattened ceratohyal, whereas in other larval and adult dissorophoids in which the ceratohyal is known, it is a rather rod-like element.

4.1.3. Branchial arches. Five branchial arches are plesiomorphic for gnathostomes (Janvier 1996), and five arches are present in coelacanths (Forey 1998), porolepiforms (Kanyukin 2006), and possibly originally also in dipnoans (Miles 1977). Thus, five branchial arches are probably also plesiomorphic for sarcopterygians. Plesiomorphically, four branchial arches are present in basal tetrapods and tetrapodomorph fishes. This configuration of the hyobranchial skeleton with the retention of four branchial arches in stem-tetrapods and basal tetrapods closely resembles that of osteichthyan fishes and larval salamanders. Only in very few taxa of basal tetrapods, is there evidence of a deviation from this pattern (see below).

In tetrapodomorph fishes, at least three (*Eusthenopteron*, Jarvik 1954, 1963) or four pairs (*Medoevia*, Lebedev 1995; *Mandageria*, Johanson & Ahlberg 1997; probably *Gogonasus*, Long *et al.* 1997; probably *Tiktaalik*, Downs *et al.* 2008) of hypobranchials are reported. These bones are stout elements and differentiated with crests and furrows, and hypobranchial 4 usually has facets for articulation with hypobranchial 3 (Lebedev 1995; Johanson & Ahlberg 1997; Long *et al.* 1997). In *Acanthostega*, no discrete hypobranchials can be found (Fig. 7b); this taxon might be specialised in the reduction of these elements or in their fusion with the ceratobranchials. This resembles the situation in dipnoans (Miles 1977) and coelacanths (Forey 1998), which normally lack discrete hypobranchials, and fusion of hypobranchials and ceratobranchials has occurred frequently in several taxa of extant salamanders (e.g. Elwood & Cundall 1994; Rose 2003). A similar situation might be present also in *Thabanchuia* (Fig. 7f), in which no hypobranchials have been found and whose ceratobranchials have similar "double headed" proximal ends, possibly for articulation with the basibranchial. The "double headed" proximal ends in fact support the hypothesis that the hypobranchials were reduced or fused with the ceratobranchials; however, it cannot be ruled out that they were cartilaginous and are simply not preserved. In colosteids, hypobranchials are short and undifferentiated (Hook 1983; this study), whereas in adelogyrinids (Fig. 7c) and lysorophians (Fig. 8e), they are long and slender. The plesiomorphic condition in

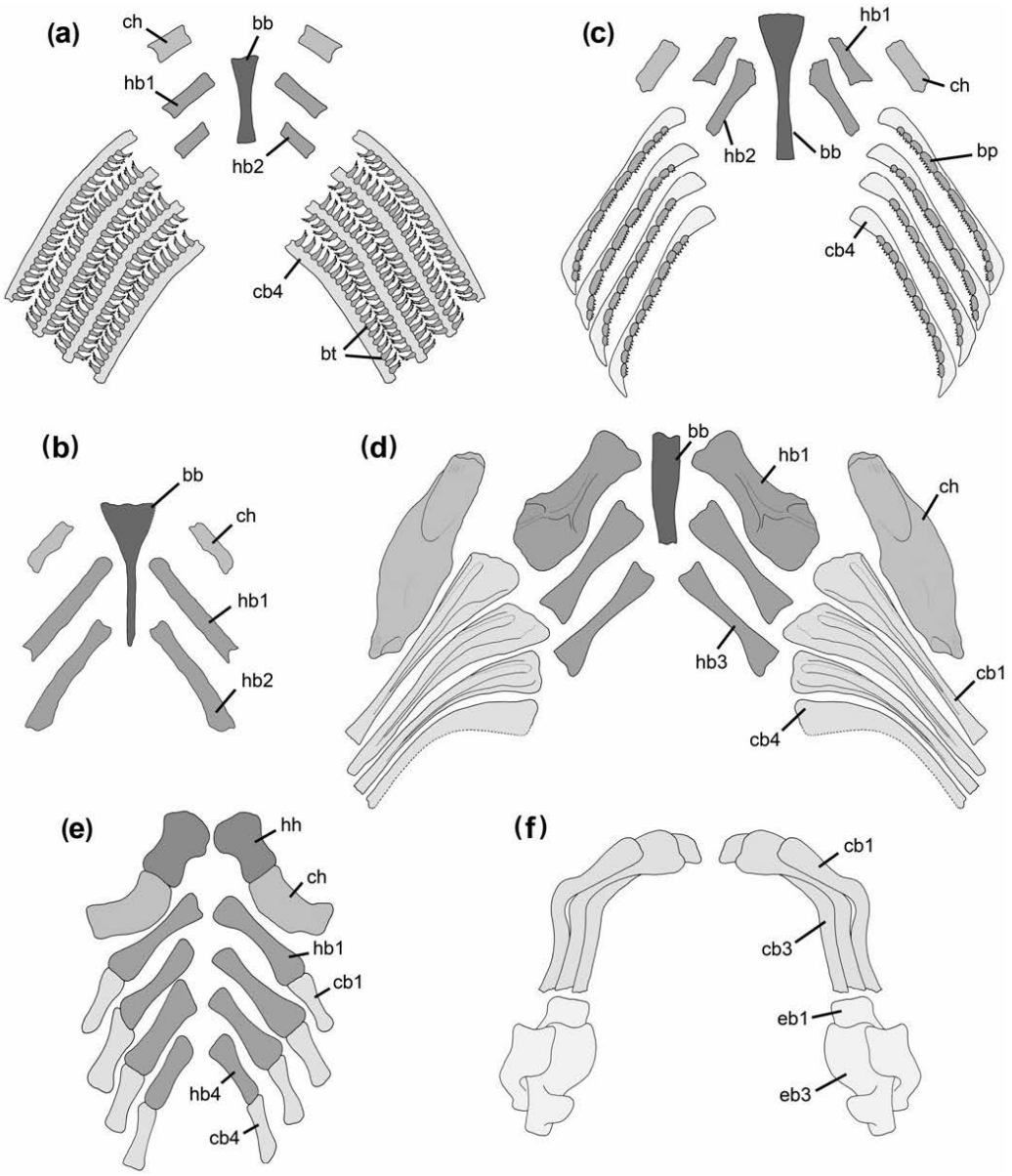

Figure 8 Reconstructions of hyobranchial apparatus in different basal tetrapods: (a) *Apateon* sp., ossified ceratobranchials and branchial teeth based on MB.Am.406, basibranchial, ceratohyal and hypobranchials supplemented after Boy & Sues (2000); (b) *Micropholis stowi*, based on BSM 1934 VIII 43; (c) *Archegosaurus decheni*, based on IGS U II 1/2 and MB.Am.983, ceratohyals and hypobranchials supplemented after Hofker (1926); (d) *Gerrothorax pulcherrimus*, based on SMNS 83866, MGUH 28919 and NRM-PZ B.18; (e) *Brachydectes elongatus*, redrawn after Wellstead (1991), "accessory bones" omitted; (f) *Pantylus cordatus*, modified after Romer (1969). Abbreviations: bb = basibranchial; bp = branchial platelets; bt = branchial teeth; cb = ceratobranchial; ch = ceratohyal; eb = epibranchial; hb = hypobranchial; hh = hypohyal.

temnospondyls is not clear, since among basal temnospondyls, *Dvinosaurus* has long, well ossified hypobranchials (Fig. 7d), whereas in *Trimerorhachis*, the bones are very short (Fig. 7e), similar to colosteids. In basal tetrapods, the hypobranchials are undifferentiated simple rods, as compared to tetrapodomorph fishes, with the exception of the first pair of hypobranchials in *Gerrothorax* (Fig. 8d) that has elaborated crests and depressions. The plesiomorphic number of hypobranchials in tetrapods is four pairs (as apparent in lysorophians; Wellstead 1991), whereas adelogyrinids (Fig. 7c) possess three pairs. Most temnospondyls have reduced the number of these bones to two pairs, with the exception of *Trimerorhachis* (Fig. 7e) and *Gerrothorax* (Fig. 8d). In extant larval or neotenic salamanders, a third and even a fourth pair of rudimentary hypobranchials may occur (Drüner 1902, 1904), and larvae of caecilians possess three pairs of hypobranchials (Stadtmüller 1936; Boy 1974). Thus, albeit there is a trend to reduce the hypobranchials to two pairs, their number is subject to variation within the different groups of basal tetrapods.

Jarvik (1954) and Downs *et al.* (2008) reported four pairs of ceratobranchials in *Eusthenopteron* and *Tiktaalik* (Fig. 7a), respectively, whereas the actual number of ceratobranchials is not known in *Medoevia* (Lebedev 1995), *Gogonasus* (Long *et al.* 1997) and *Mandageria* (Johanson & Ahlberg 1997). In tetrapods, the plesiomorphic number of ceratobranchials is likewise four pairs, as found in *Acanthostega* (Fig. 7b), lysorophians (Fig. 8e), *Dvinosaurus* (Fig. 7d), plagiosaurids (Fig. 8d), stereospondylomorphs (Fig. 8c), and at least the larvae of dissorophoids (Figs 7g, 8a), zatracheids and eryopids. The ceratobranchials of *Acanthostega*, with their curved shape and the broad, deep posterolateral groove, closely resemble those in tetrapodomorph fishes, Devonian lungfishes (Miles 1977) and porolepiforms (Kanyukin 2006; Downs *et al.* 2011). This recalls also the situation in dvinosaurian temnospondyls and adelogyrinids, with the difference that the grooves appear proportionally shallower and narrower than in *Acanthostega*. Among plagiosaurids, ceratobranchial morphology in *Gerrothorax* differs from that of other basal tetrapods and their fish-like relatives, in that they have a distinctly widened, triangular proximal portion which is flattened compared to the shaft and possesses an elaborate pattern of ridges and furrows. The different morphology of these arches in *Gerrothorax* might be associated with the general strong dorsoventral flattening of this animal. The ossified ceratobranchials in dissorophoid, zatracheid and eryopid larvae are proportionally more slender, and possess no posterolateral grooves (Witzmann 2005; Witzmann & Schoch 2006), which are also not apparent in lysorophians (Wellstead 1991).

The epibranchials, which are located distal to the ceratobranchials were demonstrated in *Eusthenopteron* (Jarvik 1954) and are probably preserved in *Gogonasus* as well (Long *et al.* 1997). The only early tetrapods with unequivocal epibranchials preserved are *Acanthostega* (Fig. 7b) (Clack & Coates 1993; Clack 2012; this study) and probably *Pantylus* (Fig. 8f). Because atavistic epibranchials may occur in individuals of extant urodele larvae (Reilly & Lauder 1988), and Elwood & Cundall (1994, fig. 9) illustrated a possible second epibranchial in *Cryptobranchus*, it can be assumed that the genetic potential to form epibranchials was obviously still present in early tetrapods.

4.1.4. Denticulated pharyngeal/branchial platelets. Teeth or denticles in the pharyngeal region are characteristic for osteichthyans (Jarvik 1980). In *Eusthenopteron*, pharyngeal bony plates of different size are present on the basibranchials, ceratohyals, hypobranchials, ceratobranchials, epibranchials and the neurocranium (Jarvik 1954, 1963). Their surface is covered by a shagreen of small teeth (denticles), whereas some larger teeth may be present along the free edges (Jarvik 1954; pers. obs. NRM PZ 2609). A very similar pattern of denticulated platelets was found in *Mandageria* (Johanson & Ahlberg 1997), whereas corresponding structures associated with hyobranchial elements were not described in *Tiktaalik* and *Acanthostega*, and it is not clear whether they are simply not preserved or were actually absent in the living animals. In early tetrapods, denticulate platelets are restricted to the cartilaginous or ossified ceratobranchials in aquatic forms with opened gill clefts (branchial platelets) (Schoch 2002; Witzmann 2004). In temnospondyls, denticulate ossified platelets are developed in the interpterygoid vacuities (Witzmann 2006, and references therein), and this might be a novel feature of this group. In contrast to these interpterygoid platelets and the pharyngeal platelets of fishes, the shagreen of denticles on the branchial platelets is reduced and the platelets bear only larger teeth at one edge (probably homologous to the large teeth along the free edge in *Eusthenopteron*). The earliest and basalmost tetrapods with preserved branchial platelets are colosteids, whose platelets are elongate and bear a large number of associated teeth on one edge. This might be the plesiomorphic morphology of branchial platelets in tetrapods, which was altered in different lineages of basal tetrapods: among dvinosaurians, stereospondylomorphs (*Sclerocephalus*, *Plagiosuchus*, *Gerrothorax*) and many dissorophoids the platelets are quadrangular rather than elongate, and branchiosaurids and trematopids have even reduced the platelets proper and modified the branchial teeth for filter feeding (Boy & Sues 2000; Milner 2007; Schoch & Milner 2008). Interestingly, no branchial teeth have ever been found in "anthracosaurs", including seymouriamorphs, although numerous specimens of larval seymouriamorphs with external gills are known (Klembara 1995; Bulanov 2003; Klembara & Ruta 2005; pers. obs.). The lack of pharyngeal teeth is enigmatic in "anthracosaurs", since the presence of external gills in larvae and the postbranchial lamina at least in *Archeria* (Pawley 2006) might suggest the presence of open gill clefts. Also in lepospondyls, no branchial teeth have ever been found, with the exception of the "microsaur" *Microbrachis* (Olori 2011). Extant amphibians have completely reduced the teeth on the branchial arches. Larval salamanders, however, possess gill rakers consisting of cartilage or connective tissue on the ceratobranchials. These gill rakers may mineralise in rare cases, as reported in larvae of the salamander, *Rhyacotriton olympicus* (Worthington & Wake 1971). Gill rakers of adjacent branchial arches interdigitate to allow the animal to close the gill clefts, in this respect resembling the configuration of branchial teeth in branchiosaurids (Carroll 2004), but gill rakers must not be confused with branchial teeth (Schoch 2001). Among caudates, branchial teeth were reported by Gao & Shubin (2012) in the Late Jurassic *Beiyanerpeton* and by Skutschas & Gubin (2012) in the Paleocene–early Eocene *Seminobatrachus*. This indicates that among lissamphibians, at least early crown-group salamanders retained teeth on the branchial arches.

4.2. Phylogenetic implications

The retention of three or four grooved ceratobranchials and/or the presence of a postbranchial lamina on the dermal shoulder girdle in several taxa give strong evidence that internal gills were widespread in stem-tetrapods and basal tetrapods. Grooved ceratobranchials *plus* a postbranchial lamina have been found in *Acanthostega* (Coates & Clack 1991) and among temnospondyls in the dvinosaurian *Thabanchuia* (this study) and the plagiosaurid *Plagiosuchus* (Schoch & Witzmann 2011). Grooved ceratobranchials, but no evidence of a postbranchial lamina, were demonstrated in *Ichthyostega* (Clack *et al.* 2003), adelogyrinids (this study), the temnospondyls *Dvinosaurus* (Sushkin 1936; Bystrow 1938; this study) and *Trimerorhachis* (Witzmann 2004; Schoch & Witzmann 2011; this study),

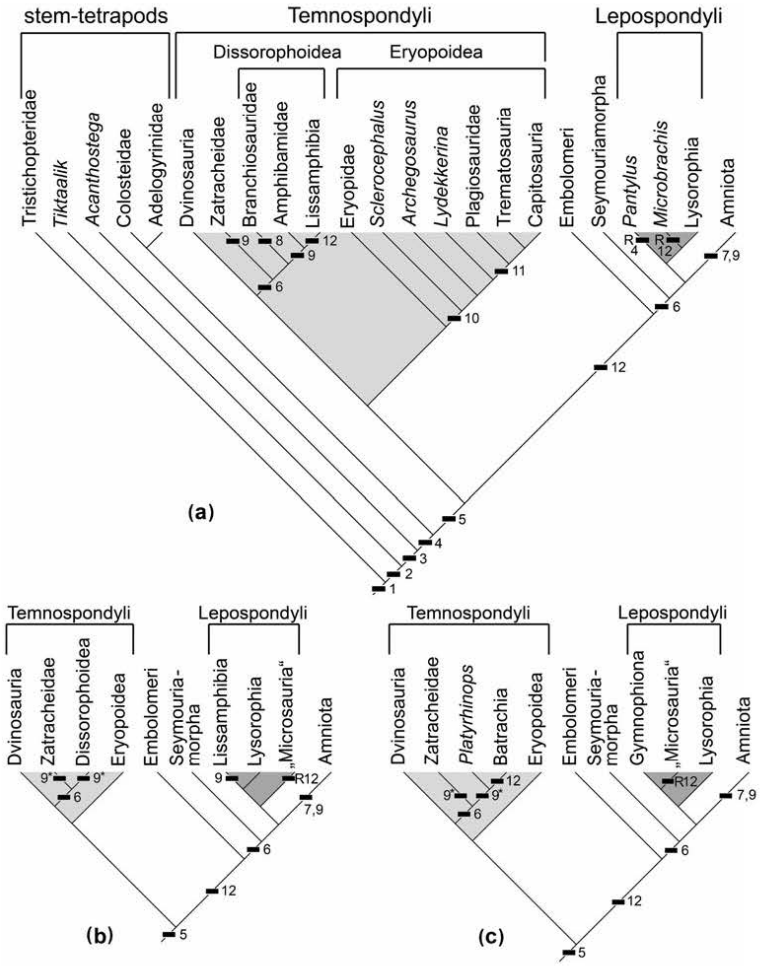

Figure 9 Hyobranchial characters plotted on different phylogenies of early tetrapods representing the temnospondyl (TH), lepospondyl (LH) and diphyly (DH) hypotheses of the origin of lissamphibians: (a) phylogeny based on Ruta & Coates (2007) and Schoch (2013), representing the TH. The clade Eryopoidea encompasses the Eryopidae and the Stereospondylomorpha; (b) phylogeny based on Marjanović & Laurin (2008), representing the LH; (c) phylogeny based on Anderson *et al.* (2008), representing the DH. Explanation of numbers: 1 = four pairs of deeply grooved ceratobranchials; internal gills; two ossified basibranchials, ceratohyals 1 and 2; 2 = pharyngobranchials reduced; single ceratohyal; 3 = not more than one basibranchial bone; pharyngeal dentition reduced to ceratobranchials; 4 = epibranchials reduced; 5 = external gills in larvae; 6 = loss of internal gills; 7 = loss of external gills; 8 = branchial teeth modified for filter feeding; 9 = remodelled "terrestrial" hyobranchium with reduced posterior branchial arches for tongue feeding in terrestrial adults; 10 = basibranchial anteriorly downturned; 11 = basibranchial morphologically simplified, not ossified in most taxa; 12 = branchial dentition reduced. Abbreviation: R = reversal. *remodelling of the adult hyobranchium must have developed independently in zatracheids and dissorophoids, since the adult hyobranchial structure of zatracheids is uniquely derived (see Witzmann & Schoch 2006).

the plagiosaurid *Gerrothorax* (Hellrung 2003; Schoch & Witzmann 2011; this study) and the stem-metoposaurid *Callistomordax kugleri* (Schoch 2008; this study). A postbranchial lamina, but no ossified ceratobranchials, is present in *Greererpeton* (Lebedev & Coates 1995), possibly *Whatcheeria* (Lombard & Bolt 1995) and *Baphetes* (Milner *et al.* 2009), the trematosaurid *Trematolestes* (Schoch & Witzmann 2011) and among "anthracosaurs" probably in *Archeria* (Pawley 2006). Taking the analyses of Ruta & Coates (2007) and Schoch (2013) as phylogenetic framework, then internal gills were reduced at least twice in tetrapod evolution (Fig. 9a): in the clade comprising the terrestrial zatracheids and dissorophoids (the latter including all lissamphibians according to the temnospondyl hypothesis (TH) of lissamphibian ancestry of Ruta & Coates 2007) and on the amniote stem below lepospondyls and seymouriamorphs, since these forms show no evidence for grooved ceratobranchials, and no postbranchial lamina either on cleithrum or the clavicle have ever been found. External gills evolved somewhere on the tetrapod stem and were retained in temnospondyl and seymouriamorph larvae and probably among microsaurs

in *Microbrachis*. Also, lysorophians, whose ceratobranchials are not grooved, might have possessed external gills, although soft tissue is not preserved (Wellstead 1991). Considering the phylogeny of Marjanović & Laurin (2008), according to which all lissamphibians are nested within lepospondyls and temnospondyls are stem-tetrapods (lepospondyl hypothesis (LH), Fig. 9b), internal gills were likewise reduced within temnospondyls (in the clade comprising zatracheids and dissorophoids) and on the tetrapod-stem below seymouriamorphs. Taking the diphyly hypothesis (DH) into account, in which batrachians are derived from dissorophoid temnospondyls and gymnophionans from "microsaurs" (Carroll 2007; Anderson *et al.* 2008), there is no apparent difference from the temnospondyl and lepospondyl hypothesis in this respect (Fig. 9c). Thus, the internal gills of early tetrapods were reduced independently within temnospondyls and on the amniote stem below seymouriamorphs, irrespective of which of the three presently discussed scenarios of lissamphibian origin is taken as a phylogenetic framework.

Retention of the third or even the fourth branchial arch (and thus of a "fish-like" or "aquatic" hyobranchium) occurred not only in primarily aquatic early tetrapods, but also in rather terrestrial forms such as the "microsaur" *Pantylus*, although internal and external gills were certainly absent in the adults. Also, the proximal and anterior hyobranchial elements (basibranchial, ceratohyals, hypobranchials) of terrestrial adult dissorophoids such as *Micropholis*, *Pasawioops* and *Doleserpeton* resemble closely the "aquatic" type (unfortunately, the ceratobranchials are not preserved in adult dissorophoids). Evidence of transformation or remodelling into a true "terrestrial" hyobranchium (i.e., with the posterior branchial arches reduced and the anteromedial hyobranchial elements modified to support a moveable tongue for terrestrial feeding) is poor in basal tetrapods; it is apparent in zatracheids and among dissorophoids in amphibamids and most probably evolved independently (Witzmann & Schoch 2006; Clack & Milner 2010). Clack & Milner (2010) suspected that the adult hyobranchial skeleton in the amphibamid *Platyrhinops* represents a primitive version of the tongue-elevating system found in salamanders and anurans and might indicate a close relationship. If this was true, then gymnophionans, who retain three or four pairs of ceratobranchials and have a poorly developed tongue musculature (Stadtmüller 1936; Wake 1989), have secondarily reduced tongue feeding. There is no evidence of a "terrestrial" hyobranchium in lepospondyls, and it is not clear if it evolved in terrestrial "anthracosaurs" such as seymouriamorphs, due to the lack of adequately preserved hyobranchial elements. Thus, taking the phylogeny of Ruta & Coates (2007) as a basis, a "terrestrial" hyobranchium evolved within temnospondyls in zatracheids and amphibamids plus lissamphibians, as well as once or several times in early amniotes or in their immediate stem-forms. This picture does not change if the DH is considered and when the poorly developed tongue musculature in gymnophionans is regarded as primitive and not as secondarily reduced. However, the LH would imply that, apart from temnospondyls and amniotes, tongue feeding evolved independently also within lepospondyls. The LH also differs from the two other hypotheses concerning the reduction of branchial dentition. On the basis of the LH, branchial dentition was lost once on the amniote stem below embolomeres (with a reversal in *Microbrachis*); according to the TH and DH, it was lost twice: among temnospondyls (in lissamphibians or batrachians, respectively) and on the amniote stem below embolomeres (with a reversal in *Microbrachis*).

The data presented in this study show that a fish-like hyobranchial apparatus was retained in early tetrapod evolution not only in early growth stages (larvae), but was present also in adults of different lineages, both primarily aquatic and terrestrial forms. Thus, three or four pairs of cartilaginous or ossified ceratobranchials in basal tetrapods do not necessarily represent a larval or paedomorphic character, respectively, as has been often suggested in analogy to extant salamanders (e.g. Bystrow 1938; Romer 1947; Watson 1956; Boy 1974; Boy & Sues 2000). Rather, it represents the plesiomorphic state of the adult hyobranchium in tetrapods.

5. Conclusions

1. The basic arrangement of hyobranchial skeletal elements has been conserved to a remarkable degree across the fish–to–tetrapod transition. The plesiomorphic condition of the tetrapod hyobranchium may be reconstructed as follows: one slender, rod-like basibranchial bone with expanded anterior and less expanded posterior portions; a pair of small, stout hypohyals; one pair of elongate, albeit flattened ceratohyals; four pairs of rod-like hypobranchials; four pairs of curved, deeply grooved ceratobranchials that bear elongate, denticulate branchial platelets; and short epibranchials.
2. The most prominent changes in the hyobranchium during the fish–to–tetrapod transition include the reduction of the number of skeletal elements, morphological simplification of basibranchial and hypobranchials, restriction of tooth-bearing pharyngeal platelets to the ceratobranchials (with loss of the denticle shagreen), reduction of the degree of ossification especially in the epiphyses of skeletal elements and reduction of ossified articulation facets.
3. The fish-like hyobranchial apparatus represents the plesiomorphic state of the adult hyobranchium in tetrapods and is not necessarily a paedomorphic character. It was retained in different lineages of basal tetrapods and was primitively associated with internal gills in adults and external gills in early growth stages. The internal gills of early tetrapods were reduced independently within temnospondyls and on the amniote stem below seymouriamorphs. The external gills were reduced in the immediate ancestors of amniotes. This is irrespective of which of the three presently discussed scenarios of lissamphibian origin (temnospondyl, lepospondyl or diphyly hypotheses) is taken as a phylogenetic framework.
4. Early tetrapods exhibit not more than one basibranchial bone, in contrast to their Devonian fish-like relatives and many extant amphibians. There might have been more than one basibranchial element in early tetrapods, from which only one element was ossified and is preserved. Alternatively, the single preserved basibranchial element might have given rise to the two or more centres as in extant amphibians.
5. Lissamphibians, "anthracosaurs", lepospondyls (with a reversal in the "microsaur" *Microbrachis*) and amniotes have lost the branchial dentition. On the basis of a phylogeny that supports the lepospondyl hypothesis, branchial dentition was reduced once on the amniote stem below embolomeres; according to phylogenies that support the temnospondyl and diphyly hypothesis, branchial dentition was lost twice: among temnospondyls in lissamphibians or batrachians, respectively, and on the amniote stem below embolomeres.
6. Evidence of remodelling of the "fish-like" hyobranchial apparatus into a true "terrestrial" one with reduction of the posterior branchial arches and modification of the anteroior and proximal parts to support terrestrial tongue feeding is scarce in early tetrapods. It evolved within temnospondyls independently in zatracheids and dissorophoids (including lissamphibians according to the temnospondyl hypothesis) as well as once or several times in early amniotes or in their immediate stem-forms above lepospondyls.
7. Future studies should focus on the homology of the medial elements in the larval hyobranchium of salamanders and caecilians with respect to the hyobranchium in basal tetra-

pods and tetrapodomorph fishes, a problem that is still not resolved. Furthermore, well preserved hyobranchia in basal tetrapods should be taken as a basis for muscle and ligament reconstruction and studies in functional morphology, using feeding behaviour and hyobranchial morphology in extant fishes and salamanders as the phylogenetic bracket.

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7. References

Anderson, J. S., Carroll, R. L. & Rowe, T. B. 2003. New information on *Lethiscus stocki* (Tetrapoda: Lepospondyli: Aïstopoda) from high-resolution computed tomography and a phylogenetic analysis of Aïstopoda. *Canadian Journal of Earth Sciences* **40**, 1071 83.

Anderson, J. S., Reisz, R. R., Scott, D., Fröbisch, N. B. & Sumida, S. S. 2008. A stem batrachian from the Early Permian of Texas and the origin of frogs and salamanders. *Nature* **453**, 515 18.

Andrews, S. M. & Carroll, R. L. 1991. The order Adelospondyli: Carboniferous lepospondyl amphibians. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **82**, 239 75.

Arratia, G. & Schultze, H.-P. 1990. The urohyal: development and homology within osteichthyans. *Journal of Morphology* **203**, 247 82.

Berman, D. S. 1973. A trimerorhachid amphibian from the Upper Pennsylvanian of New Mexico. *Journal of Paleontology* **47**, 932 45.

Bossy, K. A. & Milner, A. C. 1998. Order Nectridea. *In* Wellnhofer, P. (ed.) *Encyclopedia of Paleoherpetology, vol. 1: Lepospondyli*, 73 131. München: Verlag Dr. Friedrich Pfeil.

Bourget, H. & Anderson, J. S. 2011. A new amphibamid (Temnospondyli: Dissorophoidea) from the Early Permian of Texas. *Journal of Vertebrate Paleontology* **31**, 32 49.

Boy, J. A. 1972. Die Branchiosaurier (Amphibia) des saarpfälzischen Rotliegenden (Unter-Perm, SW-Deutschland). *Abhandlungen des Hessischen Landesamtes für Bodenforschung* **65**, 1 137.

Boy, J. A. 1974. Die Larven der rhachitomen Amphibien (Amphibia: Temnospondyli; Karbon Trias). *Paläontologische Zeitschrift* **48**, 236 82.

Boy, J. A. 1985. Über *Micropholis*, den letzten Überlebenden der Dissorophoidea (Amphibia, Temnospondyli; Unter-Trias). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1985**, 29 45.

Boy, J. A. 1988. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstes Karbon Perm). 1. *Sclerocephalus*. *Paläontologische Zeitschrift* **62**, 107 32.

Boy, J. A. 1990. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstes Karbon Perm). 3. *Onchiodon*. *Paläontologische Zeitschrift* **64**, 287 312.

Boy, J. A. 1993. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstes Karbon Perm). 4. *Cheliderpeton latirostre*. *Paläontologische Zeitschrift* **67**, 123 43.

Boy, J. A. 1995. Über die Micromelerpetontidae (Amphibia: Temnospondyli) 1. Morphologie und Paläoökologie des *Micromelerpeton credneri* (Unter-Perm; SW-Deutschland). *Paläontologische Zeitschrift* **69**, 429 57.

Boy, J. A. 2003. Paläoökologische Rekonstruktion von Wirbeltieren: Möglichkeiten und Grenzen. *Paläontologische Zeitschrift* **77**, 123 53.

Boy, J. A. & Sues, H.-D. 2000. Branchiosaurs: Larvae, Metamorphosis and Heterochrony in Temnospondyls and Seymouriamorphs. *In* Heatwole, H. & Carroll, R. L. (eds) *Amphibian Biology 4: Palaeontology*, 1150 97. Chipping Norton: Surrey Beatty and Sons.

Broili, F. & Schröder, J. 1937. Beobachtungen an Wirbeltieren der Karrooformation. XXV. Über *Micropholis* Huxley. XXVI. Über *Lydekkerina* Broom. *Sitzungsberichte der bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Abteilung* **1937**, 19 57.

Bulanov, V. V. 2003. Evolution and systematics of seymouriamorph parareptiles. *Paleontological Journal* **37** (Supplement 1), 1 105.

Bystrow, A. P. 1938. *Dvinosaurus* als neotenische Form der Stegocephalen. *Acta Zoologica* **19**, 209 95.

Carroll, R. L. 1969. A new family of Carboniferous amphibians. *Palaeontology* **12**, 537 48.

Carroll, R. L. 1998. Order Aïstopoda. *In* Wellnhofer, P. (ed.) *Encyclopedia of Paleoherpetology, vol. 1: Lepospondyli*, 163 82. München: Verlag Dr. Friedrich Pfeil.

Carrol, R. L. 2004. The importance of branchiosaurs in determining the ancestry of the modern amphibian orders. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **232**, 157 80.

Carroll, R. L. 2007. The Palaeozoic ancestry of salamanders, frogs and caecilians. *Zoological Journal of the Linnean Society* **150** (Supplement 1), 1 140.

Carroll, R. L. & Gaskill, P. 1978. The order Microsauria. *American Philosophical Society Memoirs* **126**, 1 211.

Clack, J. A. 1992. The stapes of *Acanthostega gunnari*. *In* Webster, D. B., Fay, R. R. & Popper, A. N. (eds) *The evolutionary biology of hearing*, 405 20. Berlin and Heidelberg: Springer Verlag.

Clack, J. A. 2003. A new baphetid (stem tetrapod) from the Upper Carboniferous of Tyne and Wear, U.K., and the evolution of the tetrapod occiput. *Canadian Journal of Earth Sciences* **40**, 483 98.

Clack, J. A. 2012. *Gaining ground. The origin and evolution of tetrapods.* Second edition. Bloomington and Indianapolis: Indiana University Press.

Clack, J. A., Ahlberg, P. E., Finney, S. M., Dominguez Alonso, P., Robinson, J. & Ketcham, R. A. 2003. A uniquely specialized ear in a very early tetrapod. *Nature* **425**, 65 69.

Clack J. A. & Coates, M. I. 1993. *Acanthostega gunnari* our present connection. *In* Hoch, E & Brantsen, A. K. (eds) *Deciphering the natural world and the role of museums and collections*, 39 42. Copenhagen: Geologisk Museum Press.

Clack, J. A. & Milner, A. R. 2010. Morphology and systematics of the Pennsylvanian amphibian *Platyrhinops lyelli* (Amphibia: Temnospondyli). *Transactions of the Royal Society of Edinburgh: Earth Sciences* **100**(for 2009), 275 95.

Coates, M. I. & Clack, J. A. 1991. Fish-like gills and breathing in the earliest known tetrapod. *Nature* **352**, 234 36.

Damiani, R. J. & Warren, A. A. 1997. Re-interpretation of *Parotosuchus wadei* Cosgriff, a capitosaurid from the Triassic Narrabeen Group at Gosford, New South Wales, with comments on its growth stage. *Alcheringa* **21**, 281 89.

Deban, S. M. & Wake, D. B. 2000. Aquatic Feeding in Salamanders. *In* Schwenk, K. (ed.) *Feeding: form, function and evolution in tetrapod vertebrates*, 65 94. San Diego: Academic Press.

Downs, J. P., Daeschler, E. B., Jenkins, F. A. Jr. & Shubin, N. H. 2008. The cranial endoskeleton of *Tiktaalik roseae*. *Nature* **455**, 925 29.

Downs, J. P., Daeschler, E. B., Jenkins, F. A. Jr. & Shubin, N. H. 2011. A new species of *Laccognathus* (Sarcopterygii, Porolepiformes) from the Late Devonian of Ellesmere Island, Nunavut, Canada. *Journal of Vertebrate Paleontology* **31**, 981 96.

Drüner, L. 1902. Studien zur Anatomie des Zungenbein-, Kiemenbogen- und Kehlkopfmuskeln der Urodelen. 1. Theil. *Zoologische Jahrbücher, Abteilung Anatomie und Ontogenie der Tiere* **15**, 435 622.

Drüner, L. 1904. Studien zur Anatomie des Zungenbein-, Kiemenbogen- und Kehlkopfmuskeln der Urodelen. 2. Theil. *Zoologische Jahrbücher, Abteilung Anatomie und Ontogenie der Tiere* **15**, 361 690.

Elwood, J. R. L. & Cundall, D. 1994. Morphology and behavior of the feeding apparatus in *Cryptobranchus alleganiensis* (Amphibia: Caudata). *Journal of Morphology* **220**, 47 70.

Forey, P. 1998. *History of the coelacanth fishes*. London: Chapman and Hall.

Fröbisch, N. B. & Reisz, R. R. 2008. A new Lower Permian amphibamid (Dissorophoidea, Temnospondyli) from the fissure fill deposits near Richards Spur, Oklahoma. *Journal of Vertebrate Paleontology* **28**, 1015 30.

Gao, Ke-Qin & Shubin, N. H. 2012. Late Jurassic salamandroid from western Liaoning, China. *Proceedings of the National Academy of Sciences* **109**, 5767 72.

Hellrung, H. 2003. *Gerrothorax pustuloglomeratus*, ein Temnospondyle (Amphibia) mit knöcherner Branchialkammer aus dem Unteren Keuper von Kupferzell (Süddeutschland). *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)* **330**, 1 130.

Henrici, A. C., Martens, T., Berman, D. S. & Sumida, S. S. 2011. An ostodolepid 'microsaur' (Lepospondyli) from the Lower Permian Tambach Formation of central Germany. *Journal of Vertebrate Paleontology* **31**, 997–1004.

Hofker, J. 1926. *Archegosaurus decheni* Goldfuss. Untersuchung des Schädelbaues. *Palaeontologia Hungarica* **2**, 109–30.

Hook, R. W. 1983. *Colosteus scutellatus* (Newberry), a primitive temnospondyl amphibian from the Middle Pennsylvanian of Linton. *American Museum of Natural History Novitates* **2770**, 1–41.

Ivakhnenko, M. F. 1987. [Permian parareptiles of USSR.] *Trudy Paleontologichesko Instituta Nauka SSSR* **223**, 1–160. [In Russian.]

Janvier, P. 1996. *Early vertebrates*. Oxford: Clarendon Press.

Jarvik, E. 1954. On the visceral skeleton in *Eusthenopteron* with a discussion of the parasphenoid and palatoquadrate in fishes. *Kungliga Svenska Vetenskapsakademiens Handlingar. Fjärde Serien, Band* **5**(1), 1–104.

Jarvik, E. 1963. The composition of the intermandibular division of the head in fish and tetrapods and the diphyletic origin of the tetrapod tongue. *Kungliga Svenska Vetenskapsakademiens Handlingar. Fjärde Serien, Band* **9**(1), 1–74.

Jarvik, E. 1980. *Basic structure and evolution of vertebrates, Volume 1*. London: Academic Press.

Jenkins, F. A. Jr., Shubin, N. H., Gatesy, S. M. & Warren, A. A. 2008. *Gerrothorax pulcherrimus* from the Upper Triassic Fleming Fjord Formation of East Greenland and a reassessment of head lifting in temnospondyl Feeding. *Journal of Vertebrate Paleontology* **28**, 935–50.

Johanson, Z. & Ahlberg, P. E. 1997. A new tristichopterid (Osteolepiformes; Sarcopterygii) from the Mandagery Sandstone (Famennian) near Canowindra, N.S.W., Australia. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **88**, 39–53.

Kanyukin, A. A. 2006. Hyobranchial skeleton and hypobranchial muscles of rhipidistians. *Paleontological Journal* **40**, 297–311.

Klembara, J. 1995. The external gills and ornamentation of skull roof bones of the Lower Permian tetrapod *Discosauriscus* (Kuhn 1933) with remarks to its ontogeny. *Paläontologische Zeitschrift* **69**, 265–81.

Klembara, J. & Ruta, M. 2005. The seymouriamorph tetrapod *Ariekanerpeton sigalovi* from the Lower Permian of Tadzhikistan. Part I: Cranial anatomy and ontogeny. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **96**, 43–79.

Lauder, G. V. & Reilly, S. M. 1994. Amphibian feeding behavior: comparative biomechanics and evolution. *In* Bels, M., Chardon, P. & Vandewalle, P. (eds) *Biomechanics of Feeding in Vertebrates. Advances in Comparative and Environmental Physiology, Volume 18*, 163–95. Berlin: Springer-Verlag.

Lebedev, O. A. 1995. Morphology of a new osteolepidid fish from Russia. *Bulletin du Muséum National d'Histoire Naturelle. 4e Série. Section C. Sciences de la Terre. Paléontologie, Géologie, Minéralogie* **17**, 287–341.

Lebedev, O. A. & Coates, M. I. 1995. The postcranial skeleton of the Devonian tetrapod *Tulerpeton curtum* Lebedev. *Zoological Journal of the Linnean Society* **114**, 307–48.

Lombard, R. E. & Bolt, J. R. 1995. A new primitive tetrapod, *Whatcheeria deltae*, from the Lower Carboniferous of Iowa. *Palaeontology* **38**, 471–94.

Long, J. A., Barwick, R. E. & Campbell, K. S. W. 1997. Osteology and functional morphology of the osteolepiform fish *Gogonasus andrewsae* Long, 1985, from the Upper Devonian Gogo Formation, Western Australia. *Records of the Western Australian Museum* **53**, 1–89.

Marjanović, D. & Laurin, M. 2008. A reevaluation of the evidence supporting an unorthodox hypothesis on the origin of extant amphibians. *Contributions to Zoology* **77**, 149–99.

Marjanović, D. & Laurin, M. 2013. The origin(s) of extant amphibians: a review with emphasis on the "lepospondyl hypothesis". *Geodiversitas* **35**, 207–72.

Miles, R. S. 1977. Dipnoan (lungfish) skulls and the relationships of the group: A study based on new species from the Devonian of Australia. *Zoological Journal of the Linnean Society* **61**, 1–328.

Milner, A. C., Milner, A. R. & Walsh, S. A. 2009. A new specimen of *Baphetes* from Nýřany, Czech Republic and the intrinsic relationships of the Baphetidae. *Acta Zoologica (Stockholm)* **90** (special issue), 318–34.

Milner, A. C. & Lindsay, W. 1998. Postcranial remains of *Baphetes* and their bearing on the relationships of the Baphetidae (Loxommatidae). *Zoological Journal of the Linnean Society* **122**, 211–35.

Milner, A. R. 1982. Small temnospondyl amphibians from the Middle Pennsylvanian of Illinois. *Palaeontology* **25**, 635–64.

Milner, A. R. 2007. *Mordex laticeps* and the base of the Trematopidae. *Journal of Vertebrate Paleontology* **27** (Supplement), 118A.

Nelson, G. J. 1969. Gill Arches and the Phylogeny of Fishes, With Notes on the Classification of Vertebrates. *Bulletin of the American Museum of Natural History* **141**, 477–552.

Nilsson, T. 1946. A new find of *Gerrothorax rhaeticus* Nilsson, a plagiosaurid from the Rhaetic of Scania. *Lunds Universitets Årsskrift. N.F.* **2, 42**, 1–42.

Olori, J. C. 2011. *The evolution of skeletal development in early tetrapods: anatomy and ontogeny of microsaurs (Lepospondyli)*. PhD Dissertation, Faculty of the Graduate School of the University of Texas at Austin.

Olson, E. C. 1979. Aspects of the biology of *Trimerorhachis* (Amphibia: Temnospondyli). *Journal of Paleontology* **53**, 1–17.

Olson, E. C. & Lammers, G. E. 1976. A new brachyopoid amphibian. *In* Churcher, C. S. (ed.) *Athlon: Essays on Palaeontology in Honor of Loris Shano Russell. Royal Ontario Museum Special Publication*, 45–57. Toronto: University of Toronto Press.

Pawley, K. 2006. *The postcranial skeleton of temnospondyls (Tetrapoda: Temnospondyli)*. PhD Dissertation, Faculty of Sciences, Technology, and Engineering, La Trobe University, Melbourne, Victoria.

Reilly, S. M. & Lauder, G. V. 1988. Atavisms and the homology of hyobranchial elements in lower vertebrates. *Journal of Morphology* **195**, 237–45.

Romer, A. S. 1947. Review of the Labyrinthodontia. *Bulletin of the Museum of Comparative Zoology Harvard College* **99**, 1–368.

Romer, A. S. 1969. The cranial anatomy of the Permian amphibian *Pantylus*. *Breviora* **314**, 1–37.

Rose, C. S. 2003. The developmental morphology of salamander skulls. *In* Heatwole, H. & Davies, M. (eds) *Amphibian biology, Vol. 5. Osteology*, 1686–783. Chipping Norton: Surrey Beatty and Sons.

Ruta, M. & Coates, M. I. 2007. Dates, nodes and character conflict: addressing the lissamphibian origin problem. *Journal of Systematic Paleontology* **5**, 69–122.

Schoch, R. R. 2001. Can metamorphosis be recognised in Palaeozoic amphibians? *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **230**, 335–67.

Schoch, R. R. 2002. The evolution of metamorphosis in temnospondyls. *Lethaia* **35**, 309–27.

Schoch, R. R. 2003. Early larval ontogeny of the Permo–Carboniferous temnospondyl *Sclerocephalus*. *Palaeontology* **46**, 1055–72.

Schoch, R. R. 2006. A complete trematosaurid amphibian from the Middle Triassic of Germany. *Journal of Vertebrate Paleontology* **26**, 29–43.

Schoch, R. R. 2008. A new stereospondyl from the German Middle Triassic, and the origin of the Metoposauridae. *Zoological Journal of the Linnean Society* **152**, 79–113.

Schoch, R. R. 2009. Evolution of life cycles in early amphibians. *Annual Review of Earth and Planetary Sciences* **37**, 135–62.

Schoch, R. R. 2013. The evolution of major temnospondyl clades – an inclusive phylogenetic analysis. *Journal of Systematic Palaeontology* **11**, 673–705.

Schoch, R. R. & Milner, A. R. 2000. Stereospondyli. *In* Wellnhofer P. (ed.) *Handbuch der Paläoherpetologie, Volume 3*, 1–220. München: Verlag Dr. Friedrich Pfeil.

Schoch, R. R. & Milner, A. R. 2008. The intrarelationships and evolutionary history of the temnospondyl family Branchiosauridae. *Journal of Systematic Palaeontology* **6**, 409–31.

Schoch, R. R. & Witzmann, F. 2009a. Osteology and relationships of the temnospondyl genus *Sclerocephalus*. *Zoological Journal of the Linnean Society* **157**, 135–68.

Schoch, R. R. & Witzmann, F. 2009b. The temnospondyl *Glanochthon* from the Lower Permian Meisenheim Formation of Germany. *Special Papers in Palaeontology* **81**, 121–36.

Schoch, R. R. & Witzmann, F. 2011. Bystrow's Paradox: gills, fossils, and the fish-to-tetrapod transition. *Acta Zoologica (Stockholm)* **92**, 251–65.

Shishkin, M. A. 1973. [The morphology of the early Amphibia and some problems of lower tetrapod evolution.] *Trudy Paleontologichesko Instituta Nauka SSSR* **137**, 1–257. [In Russian.]

Sigurdsen, T. & Bolt, J. R. 2010. The Lower Permian amphibamid *Doleserpeton* (Temnospondyli: Dissorophoidea), the interrelationships of amphibamids, and the origin of modern amphibians. *Journal of Vertebrate Paleontology* **30**, 1360–77.

Stadtmüller, F. 1936. Kranium und Visceralskelett der Stegocephalen und Amphibien. *In* Bolk, L., Göppert, E., Kallius, E. & Lubosch, W. (eds) *Handbuch der vergleichenden Anatomie der Wirbeltiere, Volume 4*, 501–698. Berlin and Wien: Urban und Schwarzenberg.

Skutschas, P. P. & Gubin, Y. M. 2012. A new salamander from the late Paleocene early Eocene of Ukraine. *Acta Palaeontologica Polonica* **57**, 135–48.

Steen, M. C. 1937. On *Acanthostoma vorax* Credner. *Proceedings of the Zoological Society London* **B107**, 491–500.

Sushkin, P. 1936. Notes on the pre-Jurassic Tetrapoda from USSR. III. *Dvinosaurus amalitzky*, a perennibranchiate stegocephalian from the Upper Permian from North Dvina. *Trudy Paleontologichesko Instituta Nauka SSSR* **4**, 43 91.

Van Hoepen E. C. N. 1915. Stegocephalia of Senekal, O. F. S. *Annals of the Transvaal Museum* **5**, 124 49.

Wake, M. H. 1989. Metamorphosis of the hyobranchial apparatus in *Epicrionops* (Amphibia: Gymnophiona: Rhinatrematidae): replacement of bone by cartilage. *Annales des Sciences Naturelles Zoologie* **10**, 171 82.

Warren, A. A. 1999. Karoo tupilakosaurid: a relict from Gondwana. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **89**(for 1998), 145 60.

Warren, A. A. & Hutchinson, M. N. 1988. A new capitosaurid amphibian from the Early Triassic of Queensland, and the ontogeny of the capitosaur skull. *Palaeontology* **31**, 857 76.

Warren, A. A. & Marsicano, C. 1998. Revision of the Brachyopidae (Temnospondyli) from the Triassic of Sydney, Carnarvon and Tasmania Basins, Australia. *Alcheringa* **22**, 329 42.

Warren, A. A., Rozefelds, A. C., & Bull, S. 2011. Tupilakosaur-like vertebrae in *Bothriceps australis*, an Australian brachyopid stereospondyl. *Journal of Vertebrate Paleontology* **31**, 738 53.

Watson, D. M. S. 1956. The brachyopid labyrinthodonts. *Bulletin of the British Museum (Natural History). Geology Series* **2**, 315 92.

Wellstead, C. F. 1991. Taxonomic revision of the Lysorophia, Permo-Carboniferous lepospondyl amphibians. *Bulletin of the American Museum of Natural History* **209**, 1 90.

Werneburg, R. 1991. Die Branchiosaurier aus dem Unterrotliegend des Döhlener Beckens bei Dresden. *Veröffentlichungen Naturhistorisches Museum Schleusingen* **6**, 75 99.

Werneburg, R. 1997. Der Eryopide *Onchiodon* (Amphibia) aus dem Rotliegend des Beckens von Autun (Frankreich). *Freiberger Forschungshefte* **C 466**, 167 81.

Werneburg, R. 1998. Ein larvaler *Acanthostomatops* (Zatrachydidae, Amphibia) aus der Niederhäslich-Formation (Unter-Perm) des Döhlen-Beckens. *Veröffentlichungen des Museums für Naturkunde Chemnitz* **21**, 49 52.

Werneburg, R. 2007. Der „Manebacher Saurier“ ein neuer großer Eryopide (*Onchiodon*) aus dem Rotliegend (Unter-Perm) des Thüringer Waldes. *Veröffentlichungen Naturhistorisches Museum Schleusingen* **22**, 3 40.

Witzmann, F. 2004. The external gills of Palaeozoic amphibians. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **232**, 375 401.

Witzmann, F. 2005. Hyobranchial and postcranial ontogeny of the temnospondyl *Onchiodon labyrinthicus* (Geinitz, 1861) from Niederhäslich (Döhlen Basin, Autunian, Saxony). *Paläontologische Zeitschrift* **79**, 479 92.

Witzmann, F. 2006. Cranial morphology and ontogeny of the Permo Carboniferous temnospondyl *Archegosaurus decheni* Goldfuss, 1847 from the Saar Nahe Basin, Germany. *Transactions of the Royal Society of Edinburgh, Earth Sciences* **96**(for 2005), 131 62.

Witzmann, F. & Schoch, R. R. 2006. Skeletal development of the temnospondyl *Acanthostomatops vorax* from the Lower Permian Döhlen Basin of Saxony. *Transactions of the Royal Society of Edinburgh, Earth Sciences* **96**(for 2005), 365 85.

Worthington, R. D. & Wake, D. B. 1971. Larval morphology and ontogeny of the ambystomatid salamander, *Rhyacotriton olympicus*. *The American Midland Naturalist* **85**, 349 65.

Yates, A. M. 1999. The Lapillopsidae: a new family of small temnospondyls from the early Triassic of Australia. *Journal of Vertebrate Paleontology* **19**, 302 20.

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The hyobranchial apparatus in early tetrapods and its significance for feeding and breathing

Appendix 11

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Bystrow's Paradox – gills, fossils, and the fish-to-tetrapod transition

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Abstract

Schoch, R.R. and Witzmann, F. 2011. Bystrow's Paradox – gills, fossils, and the fish-to-tetrapod transition. — *Acta Zoologica (Stockholm)* **92**: 251–265.

The issue of which breathing mechanism was used by the earliest tetrapods is still unsolved. Recent discoveries of stem tetrapods suggest the presence of internal gills and fish-like underwater breathing. The same osteological features were used by Bystrow to infer a salamander-like breathing through external gills in temnospondyl amphibians. This apparent contradiction – here called Bystrow's Paradox – is resolved by reviewing the primary fossil evidence and the anatomy of the two gill types in extant taxa. Rather unexpectedly, we find that internal gills were present in a range of early crown tetrapods (temnospondyls), based on the anatomy of gill lamellae and location of branchial arteries on the ventral side of gill arch elements (ceratobranchials). Although it remains to be clarified which components are homologous in external and internal gills, both gill types are likely to have been present in Palaeozoic tetrapods – internal gills in aquatic adults of some taxa, and external gills in the larvae of these taxa and in larvae of numerous forms with terrestrial adults, which resorbed the external gills after the larval phase. Future developmental studies will hopefully clarify which mechanistic pathways are involved in gill formation and how these might have evolved.

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Introduction

Despite numerous recent findings giving unexpected insights, the modes of respiration employed by early tetrapods remain untested. As lungs, gills and other respiratory epithelia are rarely preserved in fossils, research in this field relies almost entirely on the identification and interpretation of osteological correlates of soft-tissues. Theoretical functional considerations and phylogenetic bracketing therefore have been employed to answer this key issue in the palaeophysiology of early limbed vertebrates (Gans 1970; Romer 1972; Packard 1976; Janis and Keller 2001; Perry and Sander 2004). In recent years, new discoveries and detailed redescriptions of excellent fossil material of Devonian tetrapodomorphs (=stem tetrapods; Clack 2002a, 2006; Daeschler *et al.* 2006) have shed light on the evolution of various morphofunctional complexes, including the skull, appendicular skeleton and the hyoid arch and hyobranchium (Coates and Clack 1991, 1995; Clack 2002b; Clack *et al.* 2003; Brazeau and Ahlberg 2006; Downs *et al.* 2008). At the same time, Carboniferous and Permian tetrapod fossils have revealed much primary information on the presence and morphology of gills at least in larval forms, showing that the preservation potential of soft-tissues exists in some Palaeozoic formations (Boy and Sues 2000; Witzmann 2004, 2006).

Lungs are phylogenetically ancient organs that evolved in the osteichthyan stem group well before the first sarcopterygians invaded the land (Romer 1972; Janvier 1996). Lungs probably evolved to supply an additional source of oxygen during periods of shortage (Barrell 1916) and were thus a preadaptation for the transition to a land-living existence. The first tetrapods are therefore considered to have possessed lungs, and their existence is inferred by means of an extant phylogenetic bracket (Perry and Sander 2004). Recently, Janis and Keller (2001) have reanalysed the correlates of aerial respiration in early tetrapods, suggesting that the two-stroke buccal pump of modern amphibians (Brainerd and Ditelberg 1993) is likely to form the primitive condition for all crown tetrapods. This mechanism preceded the evolution of active aspiration observed in amniotes, which is driven by movements of the rib-cage. The ribs of most stem tetrapods and early amphibians did not permit aspiration movements (Janis

and Keller 2001). Instead, the wide skulls of many terrestrial stem-group amphibians (the temnospondyls) presumably facilitated a volumetric increase of air pumped into the lungs (Schmalhausen 1968). Although these findings indicate the importance of aerial respiration in early land-living amphibians, the majority of early crown tetrapods and limbed tetrapodomorphs (many temnospondyls, embolomeres and post-*Ichthyostega* node stem tetrapods) are likely to have had an aquatic existence (Schoch 2001, 2009). In all these taxa, the principal modes of respiration remain still unknown.

What might have been the alternative to lung breathing in these early aquatic limbed vertebrates? Again, extant amphibians are the only model for physiological inference: many of them use larval gills to breathe under water, but also employ the skin (Burggren and Infantino 1994). In all three lissamphibian clades, cutaneous respiration is significant in numerous species, both terrestrial and aquatic (Noble 1931; Wake 1966; Duellman and Trueb 1986). However, cutaneous respiration is difficult to prove in fossil taxa, and it cannot be ruled out completely in the earliest tetrapods (Clack 2002a). However, the extensive cover of dermal scales in most early tetrapods and their often large overall body size compared with extant amphibians (Witzmann 2007) make a contribution of skin to breathing unlikely (Romer 1972).

Therefore, the role of the gills in these early tetrapods comes sharply into focus. While internal gills (protected either by opercular bones in bony fishes or enlarged septa in sharks) are essential organs in all gnathostome fishes, no living tetrapod retains them, even as vestiges. Instead, gills of a different kind are found in larvae (and neotenes) of lissamphibians: instead of being located inside a gill chamber as in fishes, these gills are located outside the body surface and often form branching, bushy structures – the larvae of hynobiids, cryptobranchids and salamandrids, the sirenid and proteid neotenes and the axolotl share this type of gill, as do some caecilians (Duellman and Trueb 1986). Even in anuran tadpoles, the so-called "internal" gills are derived embryologically from such external outgrowths and are covered only secondarily by a skin fold (Gegenbaur 1901; Rauther 1937). Therefore, the gills of amphibians and fishes have been interpreted as different organs. Their homology has often been questioned because, in addition to their overall morphological differences, the relative contributions of entoderm and ectoderm are also dissimilar in the two groups (Starck 1982). At best, homology was accepted only for primordial stages of differentiation (Gegenbaur 1901; Greil 1906; Rauther 1937). These observations raise the issue of identifying the type of gills (if any) present in those taxa that spanned the fish-to-tetrapod transition.

This is the point where new palaeontological evidence comes into play. The origin of tetrapods was a process that required tens of millions of years, and the work from Clack and colleagues has shown that the time required for the transition from water to land was probably longer than formerly hypothesized (Coates and Clack 1991, 1995; Clack 2002a, 2006). In fact, the most primitive known limbed vertebrates *Acanthostega* and *Ichthyostega* appear to have been primarily aquatic animals, and their retention of internal gills has been inferred from the structure of their bony gill arch skeleton (Coates and Clack 1991; Clack 2002a). The occurrence of both fish-like internal gills and tetrapod-like limbs in these taxa is not mutually exclusive, as long as their owners were still aquatic. Presently, the (implicit) consensus seems to be that internal gills were lost after the branching of *Ichthyostega*, but before the origin of crown tetrapods (lissamphibians and amniotes). Romer, who emphasized that the evolution of limbs might have preceded the conquest of land (Romer 1958), went substantially beyond Clack's view and suggested that early crown tetrapods might have retained fish-like internal gills (Romer 1972). He was later followed by Bulanov (2003), who suggested that putative herbivorous seymouriamorphs, the kotlassiids, possessed internal gills in the adult phase. Bulanov based his assumption not on osteological correlates, but rather on the fact that gas exchange by internal gills enabled a metabolic level high enough to process herbivorous diet, in contrast to pulmonary and cutaneous respiration in which oxygen-rich and oxygen-poor types of blood are generally mixed (Bulanov 2003).

The evolutionary origin of the lissamphibian-type external gills is unknown, but fossil evidence indicates that in several groups of Palaeozoic tetrapods (temnospondyls, seymouriamorphs), external gills similar to those of salamanders were present (Boy 1974; Klembara 1995; Witzmann 2004). This is the earliest evidence for such gills in tetrapods, and there is no reason to assume that the external gills present in larvae of lepidosirenid lungfishes, although quite similar, were derived from a common ancestor of lungfishes and tetrapods (Witzmann 2004).

In conclusion, there must have been a phase in which the internal gills disappeared and the external ones evolved. It is unknown whether this involved a transformation from one gill type into another, or if one truly disappeared and was replaced by a completely new and convergent structure. So what do the fossils tell? The crux is that in early tetrapod fossils, the same morphological features have been correlated with internal *or* external gills – depending on the perspective of the researcher. From a "bottom-up" view, the hyobranchial skeleton of stem tetrapods closely resembles that of their fish-like relatives, which suggests the presence of internal gills similar to those of bony fishes (Coates and Clack 1991). From a "top-down" perspective, some of these structures are compared with the condition in salamanders (Bystrow 1938, 1939), indicating the presence of external gills! This is a problem of homology assessment but also of functional transformation in one of the most crucial evolutionary transitions in vertebrates, which we here term as "Bystrow's Paradox". Following ground-breaking work by Drüner (1902, 1904), the Russian anatomist and palaeontologist Alexei Petrovitsch Bystrow (1899–1959) described the connection among hyobranchial arches, branchial arteries and external gills in detail

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(Bystrow 1938, 1939, 1947; Fig. 1) and was among the first anatomists to infer soft anatomical traits on the basis of osteological correlates in early tetrapods.

The objectives of this study are (1) to review the soft-tissue correlates of gills in early tetrapod fossils, (2) to analyse their distribution in the tetrapod stem and early crown tetrapods, (3) to review the morphology of gills in the closest extant relatives, (4) to develop a scenario that integrates fossil evidence and phylogenetic bracketing in the most parsimonious way and (5) to formulate questions to be addressed by further developmental studies.

Materials and Methods

The following material was examined in the course of this study.

Fossil taxa: *Acanthostega gunnari* (MGUH), *Trimerorhachis insignis* (UCMP), *Dvinosaurus primus* (PIN), *Sclerocephalus haeuseri* (MB, GPIM, SMNS, PIMUZ), *Glanochthon latirostris* (MB, GPIM), *Archegosaurus decheni* (NNM, MB), *Micromelerpeton credneri* (MB, SMNS), *Apateon pedestris* (GPIM, MB, SMNS), *A. caducus* (GPIM, MB, SMNS).

Extant taxa: *Polypterus bichir* (SMNS), *Acipenser ruthenus* (SMNS), *Amia calva* (SMNS), *Latimeria chalumnae* (SMNS), *Neoceratodus forsteri* (SMNS), *Protopterus annectens* (SMNS), *Lepidosiren intermedia* (SMNS), *Amphiuma means* (MVZB, SMNS), *Ranodon sibiricus* (SIM), *Dicamptodon ensatus* (MVZB).

Abbreviations: **GPIM**, Geologisch-paläontologisches Institut, Universität Mainz, Germany; **MB**, Museum für Naturkunde Berlin, Germany; **MGUH**, Museum Geologicum Universitatis Havniensis Copenhagen, Denmark; **MVZB**, Museum of Vertebrate Zoology, Berkeley, USA; **NNM**, Naturalis Museum Leiden, The Netherlands; **PIMUZ**, Paläontologisches Institut und Museum der Universität Zürich; **PIN**, Paleontological Institute, Moscow, Russia; **SIM**, Severtsov Institute, Moscow, Russia; **SMNS**, Staatliches Museum für Naturkude Stuttgart, Germany; **UCMP**, University of California Museum of Paleontology, Berkeley, USA.

Results

Gills and osteological correlates of aquatic breathing

In addition to direct preservation of gills in fossils, a few osteological structures have been suggested to be associated with gills in osteichthyans. These are also present in the most primitive limbed taxa and, more surprisingly, in some early crown tetrapods. On discussing the implications of gill features for tetrapod evolution, we lean towards the hypothesis that temnospondyls form the stem group of lissamphibians (Ruta and Coates 2007) or at least batrachians (Anderson *et al.* 2008), but see Laurin and Reisz (1997) for an alternative view. As for sarcopterygian phylogeny, we adopt the sister-group relationship of dipnoans and tetrapods (Meyer and

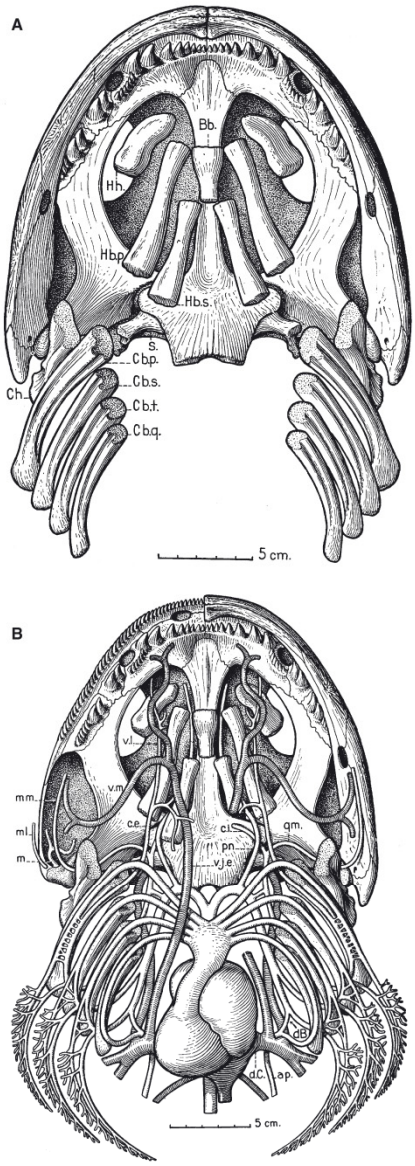

Fig. 1—Bystrow's original drawings of the skull and gill arches in *Dvinosaurus primus*, a Permian temnospondyl, in ventral view. —**A.** Skeletal reconstruction, —**B**. Restoration of blood vessels. From Bystrow (1947: figs 12, 13).

Wilson 1990; Forey *et al.* 1991), but see Fritzsch (1987) and Schultze (1991) for alternative views.

(1) *Preserved gills.* Direct preservation of gills forms the rarest of cases, but is still reported from a range of taxa. In the exceptional material of *Eusthenopteron foordi* from Escuminac Bay, Canada, internal gills are preserved (Jarvik 1980; fig. 114). In *Eusthenopteron*, the preserved hemibranch is morphologically similar to that of the extant dipnoan *Neoceratodus*, and as in other gnathostome fishes, the gill filaments reach down to the surface of the branchial arch elements. Most of the other cases of gill preservation occur within the probable stem group of lissamphibians, the temnospondyls. In contrast to *Eusthenopteron*, their gills are similar to those of extant urodeles in that they form external structures (Witzmann 2004). Unequivocal gill preservation has been confirmed in larvae of *Isodectes obtusus* (Milner 1982) (Fig. 2A), *Sclerocephalus haeuseri* (PIMUZ A II 49: a larval specimen of 25 mm skull length), *Archegosaurus decheni* (Witzmann 2004, 2006; Witzmann and Schoch 2006a) (Fig. 2B), *Micromelerpeton credneri* (Witzmann and Pfretzschner 2003) (Fig. 2C), *Branchierpeton reinholdi* (Werneburg 1988), *Apateon* spp. (Boy 1974) (Fig. 2D), *Melanerpeton humbergense* (Boy 1974), *Tungussogyrinus bergi* (Bystrow 1939; Werneburg 2009), a temnospondyl larva of uncertain affinities (Godfrey 2003) and *Amphibamus grandiceps* (Milner 1982). A possible external gill is preserved in *Platycepsion wilkinsoni* on the left side, posterior to the ceratobranchials (Warren and Marsicano 1998; Fig. 2A). Outside temnospondyls, external gills occur only in one other extinct tetrapod clade, the seymouriamorphs *Discosauriscus austriacus* (Fig. 2E), *Utegenia shpinari* and *Ariekanerpeton sigalovi* (Fig. 2F) (Ivakhnenko 1987; Klembara 1995; Bulanov 2003; Klembara and Ruta 2004, 2005). These superficially salamander-like tetrapods probably nest with embolomeres, lepospondyls and amniotes, indicating that gills must have been still present in the stem group of amniotes. On this ground, Witzmann (2004) concluded that external, salamander-like gills were present as a primitive condition in crown tetrapods.

(2) *Presence of branchial arches.* In gnathostomes, the branchial basket is formed by four elements per segment, (from ventral to dorsal) the hypo-, cerato-, epi- and pharyngobranchials (Jarvik 1980; Janvier 1996). The gills are attached to all of these elements in a crescent-like pattern, with the gill lamellae spanning approximately 180° (Rauther 1937). In lissamphibians, the dorsal portion of the branchial arches is absent, due to the lack of pharyngobranchials and epibranchials. The only exceptions are rare rudiments of epibranchials in the newt *Notophthalmus* (Reilly and Lauder 1988). In salamanders, the presence of more than two branchial arches correlates with either larval or neotenic states, and this morphological condition can be reliably taken to indicate an aquatic existence (Deban and Wake 2000; Rose 2003). The longest elements of the branchial arches are the ceratobranchials, and their presence in fossil taxa permits a comparison with osteichthyan fishes and lissamphibians. In *Acanthostega*, epibranchials are still present but pharyngo-branchials are absent (Coates and Clack 1991). In all higher taxa, only ceratobranchials (and, if ossified, hypobranchials) are reported, indicating that the absence of epi- and pharyngobranchials is a primitive condition for crown tetrapods (Schmalhausen 1968; Clack 2002a). Three or four ossified ceratobranchials are reported in the temnospondyls *Dvinosaurus* (Sushkin 1936; Bystrow 1939: 4), *Kourerpeton* (Olson 1979: 4), *Trimerorhachis* (Olson 1979; Schoch 1999; Witzmann 2004: 4), juvenile *Platycepsion wilkinsoni* (Watson 1956; Warren and Marsicano 1998: 4) larval *Branchierpeton* (Werneburg 1998: 4), larval *Acanthostomatops* (Steen 1937; Witzmann and Schoch 2006b: 3), larval *Onchiodon* (Witzmann 2005: 4), adult *Gerrothorax* (4) and *Plagiosuchus* (3 or 4), among lepospondyls in *Lysorophus* (Sollas 1920: 4) and *Adelospondylus* (Carroll and Andrews 1998: 3 hypobranchials). Imprints of cartilaginous ceratobranchials were reported in advanced larvae of *Glanochthon* (Schoch and Witzmann 2009: at least 3) and *Archegosaurus* (Witzmann 2006: 4). Ivakhnenko (1987, fig. 2) illustrated remnants of three probably cartilaginous ceratobranchials in a juvenile of the seymouriamorph *Utegenia shpinari*.

(3) *Branchial arteries.* Further significant with respect to the presence of internal gills is the posterior flank of the ceratobranchials. In extant osteichthyans, these elements are markedly grooved along their posteroventral sides (*Polypterus*: Allis 1922; *Amia*: Byczkowska-Smyk 1962 and Jarvik 1980; *Latimeria*: Forey 1998; *Neoceratodus*: Sewertzoff 1924). In these extant fishes, the grooves house one or more branches of the branchial arteries (Rauther 1937). Their occurrence in fossils is taken as evidence that the extinct species possessed branchial arteries and was therefore gill-breathing (Bystrow 1939; Witzmann 2004). Grooved ceratobranchials (Fig. 3A–D) are found in the stem tetrapods *Acanthostega* (Coates and Clack 1991) and *Ichthyostega* (Clack *et al.* 2003), and the temnospondyls *Trimerorhachis* (Olson 1979; Witzmann 2004), *Dvinosaurus* (Sushkin 1936; Bystrow 1938, 1939), *Trematolestes* (Schoch 2006), *Gerrothorax* (Hellrung 2003) and *Plagiosuchus* (observation by authors). Interestingly, the ossified ceratobranchials in larvae of *Onchiodon* (Witzmann 2005) and *Acanthostomatops* (Witzmann and Schoch 2006b), which were resorbed after the larval phase and replaced by cartilaginous elements, are round in cross section and bear no ventral grooves.

(4) *Branchial dentition.* Pharyngeal jaws are composed of tooth-bearing bonelets borne by the internal flanks of the hyobranchial elements (hypo-, cerato-, epi- and pharyngobranchials in fishes). They were reported in the ceratobranchial region of the colosteid *Colosteus* (Hook 1983),

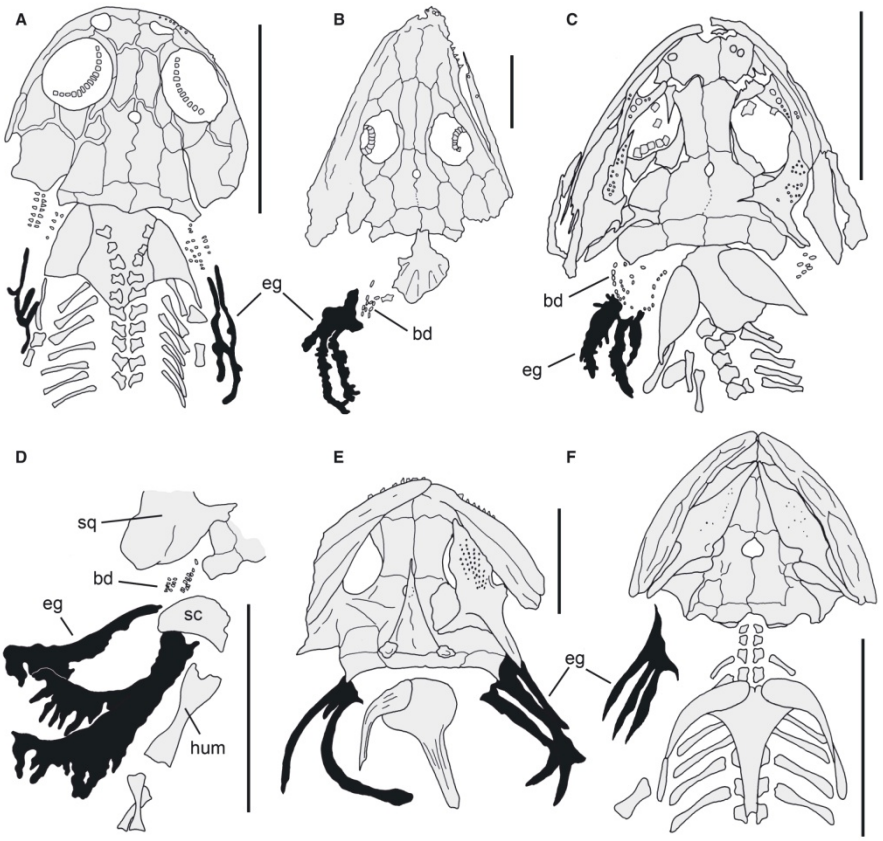

Fig. 2—Larvae of Palaeozoic tetrapods with remnants of external gills. Scale bar represents 10 mm. —**A.** *Isodectes obtusus* (Temnospondyli), redrawn after Milner (1982), —**B.** *Archegosaurus decheni* (Temnospondyli), redrawn after Witzmann (2004), —**C.** *Micromelerpeton credneri* (Temnospondyli), redrawn after Witzmann and Pfretzschner (2003), —D. *Apateon pedestris* (Temnospondyli), redrawn after Witzmann (2004), —**E.** *Discosauriscus austriacus* (Seymouriamorpha), redrawn after Werneburg (2002), —**F.** *Ariekanerpeton sigalovi* (Seymouriamorpha), redrawn after Ivakhnenko (1981). Abbreviations: bd, branchial denticles; e.g., external gills; hum, humerus; sc, scapula; sq, squamosal.

and the temnospondyls *Trimerorhachis* (Witzmann 2004), *Isodectes* (Milner 1982), *Micromelerpeton* (Boy 1972), *Branchierpeton* (Werneburg 1991), the speciose Branchiosauridae (Boy and Sues 2000), *Sclerocephalus* (Boy 1972), *Glanochthon* (Schoch and Witzmann 2009), *Archegosaurus* (von Meyer 1858; Hofker 1926; Witzmann 2004, 2006), *Uranocentrodon* (Van Hoepen 1915; Schoch 2001), *Callistomordax* (Schoch 2008), *Gerrothorax* (Nilsson 1946) and *Plagiosuchus* (present paper). By analogy with extant bony fishes, branchial denticles of fossil taxa probably indicate that the pharynx was water-filled. This adds to the first point, suggesting that branchial respiration was still practised as long as the gill clefts were open and the branchial region retained the primitive osteichthyan condition (Rauther 1937).

(5) *Branchial opening.* A postbranchial lamina, formed by a medial flange of the clavicle and cleithrum, has been interpreted as evidence of gill-breathing (Coates and Clack 1991). By analogy with fish-like sarcopterygians (Jarvik 1980; Campbell and Barwick 1986), this flange is interpreted as the posterior wall of the gill opening. However, such laminae are not always easily identified, because the cleithrum has a broadened anterior shelf in many early tetrapods, but not always a well-established flange. In extant

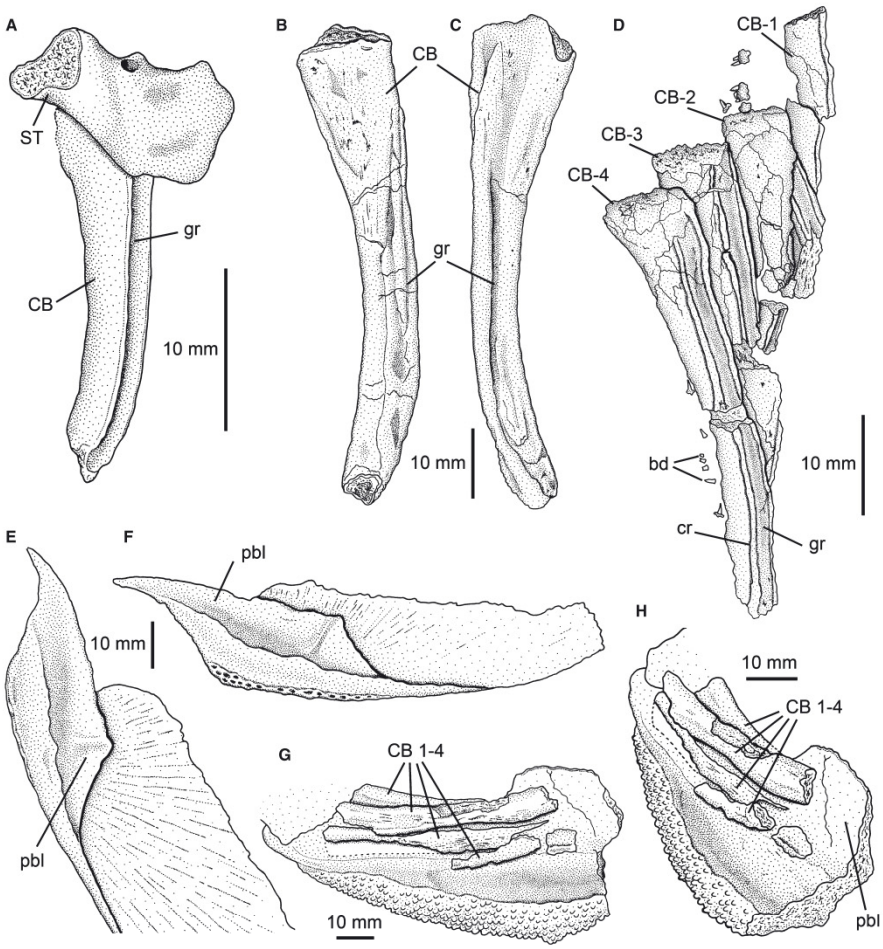

Fig. 3—Gill arch elements (ceratobranchials) of selected fossil stem and crown tetrapods. —**A**. Tetrapodomorph *Acanthostega gunnari* (MGUH f. n. 1604), —**B, C**. Temnospondyl *Gerrothorax pustuloglomeratus* (SMNS 83370) (B. Dorsal view, C. Ventral view); D. Temnospondyl *Trimerorhachis insignis* (UCMP 154434), —**E–H**. Temnospondyl clavicles with postbranchial laminae: E, F. *Trematolestes hagdorni* (SMNS 91089) (E. Anterior, F. Lateral view), —**G, H**. *Plagiosuchus pustuliferus* (SMNS 84794) (G. Anterior, H. Lateral view). Abbreviations: bd, branchial denticles; CB, ceratobranchial; cr, crest; gr, groove; pbl, postbranchial lamina; ST, stapes.

lissamphibians and amniotes, the cleithrum is reduced, and in salamanders the gill opening is not supported by a posterior bony wall. A well-defined postbranchial lamina is present in the limbed tetrapodomorph *Acanthostega* (Coates and Clack 1991) but not in *Ichthyostega* (Clack, Personal communication to FW), and in early tetrapods, it is reported in *Greererpeton* (Lebedev and Coates 1995) and probably *Baphetes* (Milner and Lindsay 1998; Milner *et al.* 2009), possibly in *Whatcheeria* [Lombard and Bolt (1995) identified a flange on the anterior edge of the lower part of the cleithrum as a postbranchial lamina; however, Coates (1996) regarded this structure as too small for a postbranchial lamina], and we have observed it on the clavicles of the temnospondyls *Plagiosuchus* and *Trematolestes* (Fig. 3E–H). (Shishkin 1987 described this structure as "lamina anterior"). In one specimen of *Plagiosuchus*, three

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or four ceratobranchials are still articulated with this lamina. The presence of a gill opening indicates a unidirectional water flow during feeding. It does not automatically indicate aquatic breathing, however, because in few extant salamanders (cryptobranchids, *Amphiuma*) unidirectional water currents are also produced by aquatic adults that have resorbed their larval gills (Deban and Wake 2000).

Anatomy of gills and branchial arches

Despite the very different anatomy of the branchial basket in hagfishes and lampreys compared with gnathostomes, vertebrate gills have recently been argued to be homologous throughout (Mallat 1984; Janvier 1996). In jawed vertebrates, these gills are always attached to the posterolateral face of the branchial arch elements, emplaced inside the body wall, and therefore called *internal gills* (Gegenbaur 1901; Goette 1901; Rauther 1937). Notwithstanding their universal presence in both cartilaginous and bony fishes, these gills vary in size, number, position and the structures covering them. For instance, in sharks, the gill septae are large and cover the gills by forming successive, overlapping gill covers, giving each gill cleft a separate opening (Rauther 1937). In bony fishes instead, there is an extensive bony cover, supported by the opercular and gular series of dermal bones, which articulate with hyoid arch elements and leave only one large opening at the posterior end of the gill region (Goodrich 1930; Rauther 1937). Despite this variation, internal gills are universal and essential for the ventilation of gnathostomes, although they may be accompanied by primitive lungs (*Polypterus*, lungfishes), an air-filled labyrinth organ (anabantoid teleosts) or numerous other respiratory epithelia in the pharynx, stomach or intestine in teleosts.

The anatomy of vertebrate gills was described by Gegenbaur (1901), Rauther (1937, 1940) and Bertin (1958). In the following section, we briefly summarize the main features and differences between internal and external gills.

Internal gills. The plesiomorphic condition for gnathostomes is to house the gills inside the body wall, attached to the branchial arches (Fig. 4A, B); only in larvae of a few taxa do filaments of these internal gills protrude the branchial opening (Rauther 1937). Internal gills agree in many features across gnathostomes, despite broad taxonomic and clade-specific variation. Internal gills are known from all gnathostome fishes, including lepidosirenid lungfishes which in addition have external larval gills (see below). Internal gills are absent in all extant crown tetrapods. The branchial region is composed of the following structures.

- *Gill lamellae* are long, vascularized sheets of tissue in which the respiratory gas exchange takes place. They form numerous parallel, closely spaced lobes attached to the posteroventral flank of the branchial arch elements (hypo-, cerato-, epi- and pharyngo-branchials). The lamellae are clearly separated from the septum which divides the anterior and posterior lamellae of each branchial arch. A single sheet of lamellae (*Kiemenblatt* of Rauther 1937) is also referred to as *branchion* (Sewertzoff 1924).
- *Gill septa* are layers of connective tissue that separate the anterior and posterior gill lamellae of each branchial arch. The posterior lamella of a given arch and the anterior lamella of the subsequent arch are thus located in the same cleft. In sharks, the septum is much longer than the lamellae and forms a flexible, valve-like cover for each gill cleft. In osteichthyans, the basic organization is the same, but all gill arches are enclosed by a large branchial chamber, which is covered laterally by a bony plate (the operculum). Rauther (1937) suggested that the operculum is derived from the septum of the hyoid arch. The septa of osteichthyans are as long as the lamellae (*Latimeria*, *Neoceratodus*), but usually shorter or even rudimentary.
- *Gill arteries* are divided into efferent and afferent branches, connected by one loop in each gill lamella. In gnathostome fishes, the efferent artery runs in a groove at the posteroventral flank of the gill arch elements.
- *Gill rays* are cartilaginous (sometimes bony) rods that develop inside the septum, known from both elasmobranchs and actinopterygians, but not from sarcopterygians (Rauther 1937).
- *Gill rakers* are anterodorsal spike- or lamella-like projections of the branchial arch into the pharyngeal chamber. In many elasmobranchs and osteichthyans, they are cartilaginous, but they may also ossify or remain entirely soft. They are often argued to form interlocking "teeth" with the neighbouring arches, but are sometimes also suggested to form a sieve-like apparatus (*Siebfortsätze* of Rauther 1937).
- *Pharyngeal jaws* are composed of numerous ossicles (small bony plates) that bear teeth; these ossicles are emplaced on the epithelial cover of the branchial arch elements. They are located in rows on the medial side of the arch, opposite to the septum and lamellae and alternating with the gill rakers. They are not identical with gill rakers and not homologous, because they have no cartilaginous precursor. That is, unlike the entodermal gill rakers, the pharyngeal jaw elements are of ectodermal origin. In osteichthyan fishes, pharyngeal jaws are involved in the maceration of prey and the transport of food from the buccal cavity into the oesophagus (Lauder and Wainwright 1992).

External gills. Although lacking *internal* gills, the larvae of many modern amphibians have filamentous outgrowths of the septum referred to as *external* gills that serve as additional respiratory organs (Rauther 1937; Schmalhausen 1955). It is generally thought that salamanders exemplify the primitive condition among lissamphibians, with three long pairs of external gills protruding the body wall in the neck region. These gills are sometimes quite similar to internal gills of osteichthyans, and their homology has been repeatedly discussed (Gegenbaur 1901; Goette 1901; Greil 1906; Sewertzoff 1924;

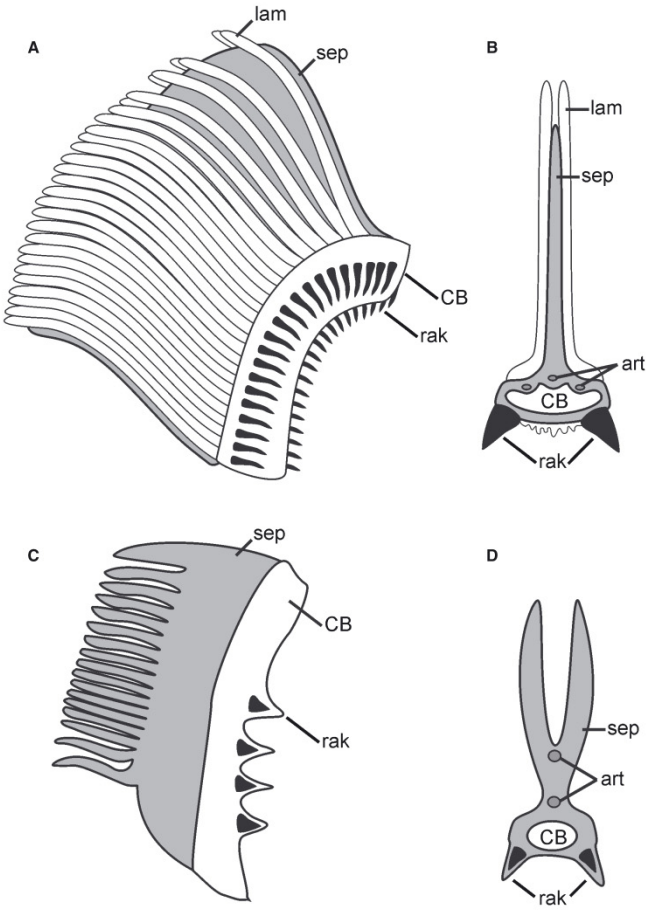

Fig. 4—Comparison of internal and external gills, —**A**. Internal gill of *Neoceratodus forsteri* (lateral view), —**B**. Transverse section of A, —**C**. External gill of *Dicamptodon ensatus* (lateral view), —**D**. Transverse section of C. Abbreviations: art, branchial artery; CB, ceratobranchial; lam, gill lamella; sep, gill septum; rak, gill raker.

Rauther 1937; Schmalhausen 1955). During metamorphosis, the external gills are resorbed in salamanders and anurans, whereas they are resorbed or lost by breakage in caecilians with aquatic larvae (Duellman and Trueb 1986). Eventually, the external gills are replaced functionally by the lungs which start to develop before or during transformation (Wilder 1925; Burggren and Infantino 1994). An exception is the highly derived plethodontid salamanders, which never develop lungs and whose adults rely completely on cutaneous and buccopharyngeal respiration (Duellman and Trueb 1986).

- As in gnathostome fishes, lissamphibian gills are attached to ceratobranchials (Fig. 4C, D); epi- and pharyngobranchials are absent. In some salamanders (*Ranodon*, *Dicamptodon*), the morphology of the external gills is quite similar to the fish condition in the morphology of the (remaining) branchial arch, the presence of gill rakers and the presence of a large, sheet-like septum. The major difference of the fish condition is that the gill lamellae are not attached to the ceratobranchial, but arise from the septum proper. The distal edge of the septum is serrated to form gill lamellae that are very similar to the ones of internal gills. As in fishes, these lamellae are paired, i.e., the septum gives rise to an anterior and a posterior lamella at each point (Schmalhausen 1968). This condition resembles the holobranch of the internal gills, although as such it is not homologous, because the lamellae have a different position and originate from the septum.
- As in fishes, *gill arteries* are divided into efferent and afferent branches, connected by one loop in each gill lamella.

In contrast to internal gills, these arteries are not located in close neighbourhood to the branchial arches, because the base of the much shorter lamellae is far away from the arch elements. Therefore, lissamphibian ceratobranchials are not grooved as those of osteichthyans and thus resemble those of larval *Onchiodon* and *Acanthostomatops* (Witzmann 2005; Witzmann and Schoch 2006b). Instead, the arteries run along the bases of the lamellae, at a considerable distance from the branchial skeleton.

- Skeletal *gill rays* are absent in lissamphibian septa, and their complete absence in Palaeozoic tetrapods suggests they were lost in the tetrapod stem.
- *Gill rakers* are present in many salamander larvae, but they are not always cartilaginous. Instead, they may also be formed by connective tissue, although this assumes a similar shape as in the cartilaginous versions.
- *Pharyngeal jaws* are never observed in lissamphibians, but Rauther (1937) hypothesized that diverticulae in the pharynx of salamander and anuran larvae might be early developmental stages of tooth germs homologous to the pharyngeal teeth of osteichthyans. At any rate, the existence of such teeth in many temnospondyls, including the lissamphibian-like branchiosaurids and amphibamids, indicates that this apparatus is primitive for lissamphibians.

Resolving the paradox

When the available fossil evidence and the anatomy of gills in modern taxa are compared, a new picture arises. We shall argue below that the new data make it possible to resolve Bystrow's Paradox, and to develop a modified interpretation of early tetrapod gills.

A strong argument has always been the claim that internal and external gills were completely different, non-homologous organs. However, in contrast to mere topographical criteria (location, internal structure), detailed observations on the development of gills do not seem to permit a straightforward rejection of their homology. Gegenbaur (1901) still distinguished then-believed entodermally formed internal gills from ectodermally built external gills of dipnoan and lissamphibian larvae. Instead, Goette (1901), Moroff (1904), Sewertzoff (1924) and Rauther (1937) reported evidence that all gnathostome gills are of the same origin, either entodermal or ectodermal, or that they combine an ectodermal component with an entodermal origin. All of these authors stressed that all gnathostome gills display striking similarities in many morphological and histological features. Schmalhausen (1955, 1968) concluded from Sewertzoff's (1924) findings that all gills were of ectodermal origin and argued for a partial homology of lissamphibians gills with those of fishes: the arch elements, septum and arteries were homologous, the early anlagen were similar, but the position of the lamellae was different. Hence, the profound similarity of lamellae in fishes and lissamphibians should be convergent. Our review of all these features confirms this view, but we do recognize the need to re-examine the development of gills in detail.

In addition, other observations have complicated matters further. For instance, externally projecting gill filaments in the branchial arches are known from the two actinopterygians *Gymnarchus* (Budgett 1901; Assheton 1907) and *Heterotis* (Daget 1957; Hermens *et al.* 2007). These gills appear to have a respiratory function, but they are not the same as external gills of lissamphibians. Likewise, in sharks, externally projecting gill filaments are confined to the embryonic period when they have both respiratory and food-absorbing functions (Bertin 1958; Pelpster and Bemis 1992). In some elasmobranchs, these gills may almost reach body length (Dohrn 1884; Rauther 1937). All these structures differ from external gills of lissamphibians in that they are topologically internal gills, with lamellae attached to the branchial arches that are simply very much elongated. In contrast to lissamphibian gills, they do not rise from the septum, but form extremely elongated lamellae consistent with those of internal gills (Rauther 1937).

A second problem is that of convergence: similar to lissamphibians, some extant lungfishes have external gills. However, internal gills similar to those of *Latimeria* are always present in dipnoans, although their number varies. *Neoceratodus* has four complete holobranchs, whereas *Protopterus* and *Lepidosiren* retain only two fully established holobranchs (Rauther 1937). In contrast to *Neoceratodus*, the lepidosirenids also have external gills, at least as larvae. Notably, they are not simple extensions of the internal gills, but form in a similar way as lissamphibian gills as outgrowths of the gill septum. Therefore, a given branchial arch either has internal or external gills, but not both. This suggests that, at least in dipnoans, the external gills formed as alternative respiratory structure and did not evolve from internal gills. Thus, in dipnoans, internal and external gills are not strictly homologous, because they develop from different tissues and there is no evidence how external gills may evolve from internal ones.

In lissamphibians, the condition is quite similar to that of lungfishes (Rauther 1937, 1940). That said, it is highly unlikely that dipnoans and tetrapods had a common ancestor with external gills; the gills of modern amphibians probably evolved in the stem group of tetrapods, were retained in many extant amphibians and lost on the amniote stem (Witzmann 2004). The origin of an external gill was possible only after the opercular bone series had been largely reduced. The extant *Neoceratodus* still retains the plesiomorphic condition (internal gills, opercular bone) and lacks external gills (Gegenbaur 1901; Rauther 1937). The Palaeozoic dipnoans had a full set of opercular elements, similar to those of other sarcopterygians (Campbell and Barwick 1986). There seems to be little space in such an apparatus for the development of an external gill, let alone several pairs. Likewise, the tetrapodomorph fishes *Eusthenopteron* and *Panderichthys*, which are more closely related to tetrapods than lungfishes are, retained complete opercular bones and therefore did not possess external gills

either. Schultze (1984) showed that even juveniles of *Eusthenopteron* had fully formed opercular bones, which rules out that external gills evolved at an early ontogenetic stage.

The view that external gills evolved in the stem group of tetrapods is not controversial and has been implicitly accepted by many authors (Fig. 5). In contrast, the persistence of internal gills in crown tetrapods appears to be more of a heresy. In part, this may be so because Romer's (1972) first speculation about this alternative either was not taken seriously or was overread. Coates and Clack's (1991) discovery of evidence for internal gills was already unexpected and added to a new interpretation of limbed tetrapodomorphs as aquatic animals. The persistence of the very same features in other stem tetrapods and temnospondyls is more unexpected still and forms a challenge to our very own picture of early tetrapod evolution. We have argued above that grooved ceratobranchials are always associated with branchial arteries in extant taxa, and they indicate the presence of gill lamellae attached with their bases to these arch elements. This infers the presence of internal gill lamellae similar to those of dipnoans and *Latimeria*, and this is the crucial point that resolves Bystrow's Paradox. In modelling his reconstruction of *Dvinosaurus* on a salamander (*Ambystoma*), Bystrow (1938) took the wrong perspective. The continuity of fish-like characters is much stronger than most workers in the field could imagine. However, Bystrow was not completely wrong about the existence of external gills. Indeed, the dvinosaurian *Isodectes*, along with a range of other related temnospondyls, did have external gills as a small larva, as found and described by Milner (1982). This shows that external and internal gills at least co-existed in the same clade, but we cannot know the ontogeny of internal gills in temnospondyls, because the grooved ceratobranchials ossified only at later stages.

The resolution of Bystrow's Paradox also sheds light on the often disputed question of how many gills were present in basal tetrapods (Sushkin 1936; Bystrow 1939; Schmalhausen 1955, 1968; Boy 1974; Witzmann 2004). As *Dvinosaurus* has four pairs of grooved ceratobranchials, Sushkin (1936) and later Schmalhausen (1968) suggested four (external) gills in the living animal. Bystrow (1939) – in a "top-down" perspective – argued for three pairs of external gills in *Dvinosaurus*, as both salamander larvae and the then newly discovered branchiosaurid *Tungussogyrinus* possess three pairs of external gills. Our new data suggest that *Dvinosaurus* indeed possessed four pairs of gills, but *internal* ones. The number of grooved ceratobranchials in other adult early tetrapods and stem tetrapods suggests three or four pairs of internal gills. In contrast, in taxa with soft-part preservation of external gills, not more than three pairs of gills are discernable, similar to larvae of lissamphibians (Witzmann 2004).

The presence of internal gills in comparably large adults of early tetrapods is biologically more meaningful than the presence of external gills. As argued by Schmalhausen (1968), external gills are disadvantageous in large animals because these delicate, exposed structures are easily vulnerable to predators and mechanical damage. As bony opercular plates were reduced in limbed tetrapodomorphs, it can be assumed that the internal gills of early tetrapods were covered by a skin fold (an "operculum" *sensu lato*, formed by connective tissue) that protected the gills. This is supported by soft-part preservation of a thick skin fold in the branchial region of *Dvinosaurus* (Sushkin 1936), and Hellrung (2003) reported a bony gill chamber in *Gerrothorax*. Similarly, although lacking any remains of bony gill arches, the largest specimen of *Isodectes* (*Sauerpeton*) *obtusus* in the United States National Museum in Washington shows a series of smooth wrinkles on each side between quadrates and clavicles. These might be interpreted as imprints of an operculum formed by connective tissue (A. R. Milner, Personal communication 2010).

Conclusions

1. A review of the visceral apparatus in Palaeozoic stem and crown tetrapods reveals that the ceratobranchial elements of the gill arches may bear important osteological correlates of soft anatomical structures. First-hand examination of extant fishes confirms the reliability of these correlates. (i) Grooves on the posterolateral flank of the ceratobranchials indicate the presence of branchial arteries, and (ii) a postbranchial lamina on the clavicle (and cleithrum) indicates the presence of a branchial opening. In addition, the presence of pharyngeal jaws (dentigerous plates on the gill arch elements) suggests at least that the pharynx was water-filled, although this need not correlate with the presence of gills.
2. Features correlated with internal, fish-like gills are more widespread among Palaeozoic tetrapods than previously thought. According to these findings, internal gills were present in a range of adult, aquatic temnospondyls. This is suggested by grooved ceratobranchials, indicating at least retention of the fish-like arterial system in some crown tetrapods. This includes one or two grooves for the efferent arteries. The close location of gill arch and arteries matches the situation in fishes, where the gill lamellae reach proximally near to the branchial arch elements. Therefore, internal gills similar to those of *Latimeria* and *Neoceratodus* are likely to have existed in taxa possessing such grooved ceratobranchials. However, these taxa differ from fishes in that the dorsal components of the branchial arch are absent, and the range of gills restricted to the ventral and lateral part of the cervical region. In *Acanthostega*, the dorsal portion was still present, albeit incomplete; a reduction of the dorsal part is likely to have been completed in crown tetrapods.
3. Direct preservation of external gills is reported in a range of Palaeozoic crown tetrapods, confirming earlier views that they must have been present in (at least the larval stages of) the earliest crown tetrapods. These external gills resemble those of basal salamanders and are probably their phylogenetic precursors.

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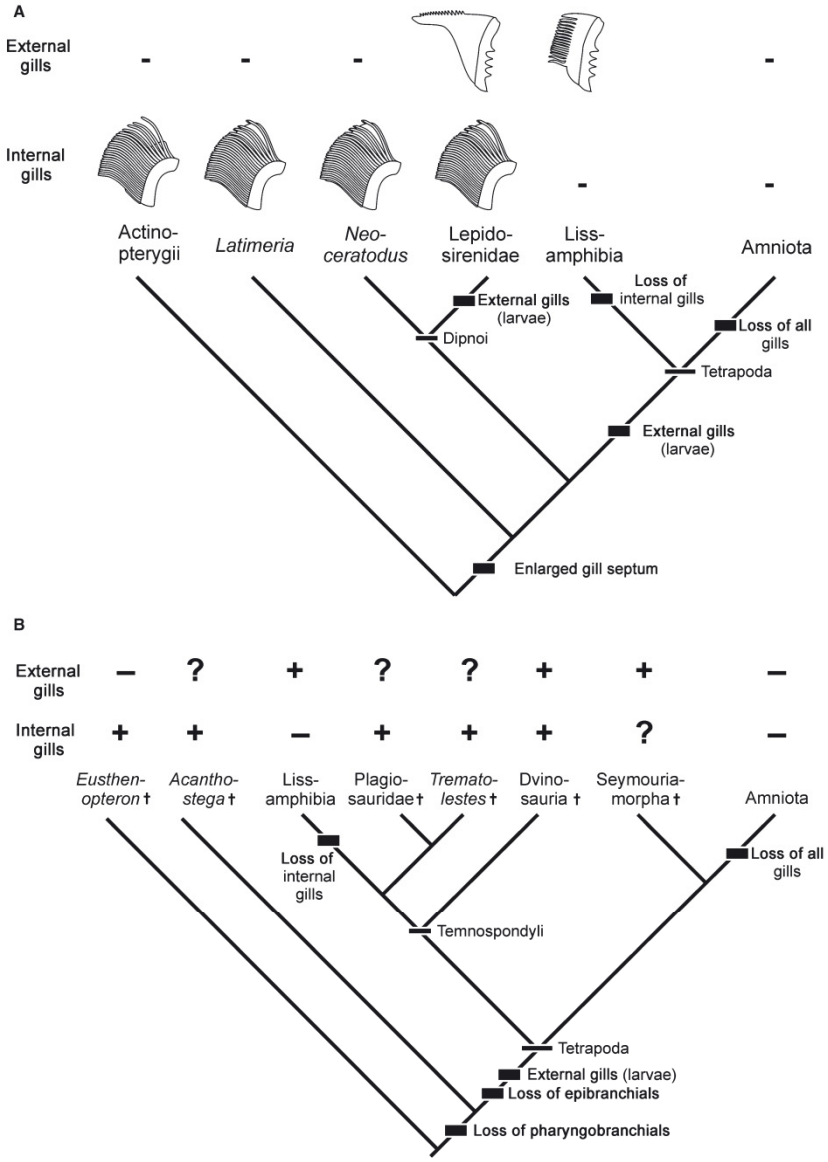

Fig. 5—Distribution of branchial gill types in vertebrates. —**A**. Phylogeny of extant osteichthyans, showing the presence and evolution of internal and external gills, —**B**. Phylogeny of tetrapodomorphs, tabulating the evidence for different gill types in fossil and extant taxa. Note that larvae of the basal actinopterygian *Polypterus* have a single external gill on the hyoid arch, which is not homologous to external gills of dipnoans or tetrapods.

4. Bystrow's Paradox – the question whether early tetrapods had internal or external gills – does not completely depend on the view of the researcher (fish or salamander-focused), but can be resolved by examination of osteological features. Our results suggest that the distribution of internal and external gills is different from what was thought before: internal gills did not disappear before the external ones evolved. This parallels the situation in lungfishes: in *Lepidosiren* and *Protopterus*, both internal and external gills are present. In early tetrapods, this appears to have occurred convergently to dipnoans. However, we do not yet know any taxon in which both gills co-existed, although internal and external gills are likely to have existed in the same clade, the dvinosaurians: larval *Isodectes* had three pairs of external gills, whereas adult *Trimerorhachis* and *Dvinosaurus* probably had four pairs of internal gills. In the Triassic stereospondyls, internal gills are likely to have existed in plagiosaurs and trematosaurs.
5. The external gills of lissamphibians form outgrowths of the gill septum, which is probably homologous to that of gnathostome fishes. Hynobiid, ambystomatid and especially dicamptodontid salamanders have gills that superficially resemble internal gills of fishes more than the bushy gills of other lissamphibians do. These similarities are (1) the relatively high number of lamellae (up to 25 in *Dicamptodon*), (2) the presence of paired lamellae (anterior, posterior), (3) the size and morphology of the septum. Extant sarcopterygians – *Latimeria*, *Neoceratodus* and lissamphibian larvae – all share long gill septa, whereas in most actinopterygians, the septum is much shorter than the gill lamellae. If this character is indeed a shared-derived state, then the formation of lamellae at the end of the septum would only be a final step towards the lissamphibian condition. Hence, external gills could be derived from internal ones, although the lamellae themselves are probably not homologous.
6. The ceratobranchials and the associated internal gills obviously represent quite conservative structures. They were not altered during the fish-to-tetrapod transition and thus do not reveal a phylogenetic signal.
7. Future studies should focus on the embryonic formation of the different components of gills in both fishes and amphibians. After the visceral arches have been shown to form from the same neural crest cells in lungfishes and salamanders (Ericsson *et al.* 2008), it would be of interest to trace the fate of cells that give rise to the septum, gill lamellae and arteries in both groups. Such studies would connect to those of Sewertzoff (1924) and Schmalhausen (1955, 1968), which already reported the various morphological changes in the development of gills. Only developmental studies can reveal (i) the homology of tissue layers in the gill region, (ii) the mechanisms of gill formation and (iii) form the basis for a model of how – and why – internal gills evolved into external ones.

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References

Allis, P. 1922. The cranial anatomy of *Polypterus*, with special reference to *Polypterus bichir*. – *Journal of Anatomy* **56**: 189–291.

Anderson, J. S., Reisz, R. R., Scott, D., Fröbisch, N. B. and Sumida, S. S. 2008. A stem batrachian from the Early Permian of Texas and the origin of frogs and salamanders. – *Nature* **453**: 515–518.

Assheton, R. 1907. *The Development of Gymnarchus niloticus*. Budgett Memorial Volume, London, 293–421.

Barrell, J. 1916. Influence of Silurian-Devonian climates on the rise of air-breathing vertebrates. – *Bulletin of the Geological Society of America* **27**: 387–436.

Bertin, L. 1958. Organes de la respiration aquatique. In: Grassé, P. P. (Ed.): *Traité de Zoologie*, vol. 13, fasc. 2, pp. 1303–1341. Masson, Paris.

Boy, J. A. 1972. Die Branchiosaurier (Amphibia) des saarpfälzischen Rotliegenden (Perm, SW-Deutschland). – *Abhandlungen des hessischen Landesamts für Bodenforschung* **65**: 1–137.

Boy, J. A. 1974. Die Larven der rhachitomen Amphibien (Amphibia: Temnospondyli, Karbon–Trias). – *Paläontologische Zeitschrift* **48**: 236–268.

Boy, J. A. and Sues, H. D. 2000. Branchiosaurs: larvae, metamorphosis and heterochrony in temnospondyls and seymouriamorphs. In: Heatwole, H. and Carroll, R. L. (Eds): *Amphibian Biology*, volume 4: *Palaeontology*, pp. 1150–1197. Surrey Beatty, Chipping Norton.

Brainerd, E. L. and Ditelberg, J. 1993. Lung ventilation in salamanders and the evolution of vertebrate air-breathing mechanisms. *Biological Journal of the Linnean Society* **49**: 163–183.

Brazeau, M. D. and Ahlberg, P. E. 2006. Tetrapod-like middle ear architecture in a Devonian fish. – *Nature* **439**: 318–321.

Budgett, J. S. 1901. On the breeding-habits of some West-African Fishes, with an account of the external features in the development of *Protopterus annectens*, and a description of the larva of *Polypterus lapradei*. – *Transactions of the Zoological Society London* **16**: 115–136.

Bulanov, V. 2003. Evolution and systematics of seymouriamorph parareptiles. – *Paleontological Journal* **37**(Suppl. 1): 1–105.

Burggren, W. W. and Infantino, R. L. 1994. The respiratory transition from water to air breathing during amphibian metamorphosis. – *American Zoologist* **34**: 238–246.

Byczkowska-Smyk, W. 1962. Vascularization and size of the respiratory surface of gills in *Acipenser stellatus* Pall. – *Acta biologica cracoviensis* **5**: 303–315.

Bystrow, A. P. 1938. *Dvinosaurus* als neotenische Form der Stegocephalen. – *Acta Zoologica* **19**: 209–295.

Bystrow, A. P. 1939. Blutgefässystem der Labyrinthodonten. (Gefässe des Kopfes). – *Acta Zoologica* **20**: 124–155.

Bystrow, A. P. 1947. Hydrophilous and xerophilous labyrinthodonts. – *Acta Zoologica* **28**: 137–164.

Campbell, K. S. W. and Barwick, R. E. 1986. Paleozoic lungfishes – a review. – *Journal of Morphology Supplement* **1**: 93–131.

Carroll, R. L. and Andrews, S. M. 1998. Order Adelospondyli. In Wellnhofer, P. (Ed.): *Encyclopedia of Paleoherpetology*, volume 1: *Lepospondyli*, pp. 149–162. Verlag Friedrich Pfeil, München.

Clack, J. A. 2002a. *Gaining Ground. The Origin and Evolution of Tetrapods*. Indiana University Press, Bloomington.

Clack, J. A. 2002b. Patterns and processes in the early evolution of the tetrapod ear. – *Journal of Neurobiology* **53**: 251–264.

Clack, J. A. 2006. The emergence of early tetrapods. – *Palaeogeography, Palaeoclimatology, Palaeoecology* **232**: 167–189.

Clack, J. A., Ahlberg, P. E., Finney, S. M., Dominguez Alonso, P., Robinson, K. and Ketcham, R. A. 2003. A uniquely specialized ear in a very early tetrapod. – *Nature* **425**: 65–69.

Coates, M. I. 1996. The Devonian tetrapod *Acanthostega gunnari* Jarvik: postcranial anatomy, basal tetrapod relationships and patterns of skeletal evolution. – *Transactions of the Royal Society of Edinburgh, Earth Sciences* **87**: 363–421.

Coates, M. I. and Clack, J. A. 1991. Fish-like gills and breathing in the earliest known tetrapod. – *Nature* **352**: 234–236.

Coates, M. I. and Clack, J. A. 1995. Romer's gap: tetrapod origins and terrestriality. – *Bulletin du Muséum national d'Histoire naturelle Paris* **17**: 373–388.

Daeschler, E. B., Shubin, N. H. and Jenkins, F. A. Jr 2006. A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. – *Nature* **440**: 757–763.

Daget, J. 1957. Mémoires sur la biologie des poissons du Niger moyen. III. Reproduction et croissance d'Heterotis niloticus Ehrenberg. – *Bulletin de l'Institut Francaise de l'Afrique Noire* **19**: 295–323.

Deban, S. M. and Wake, D. B. 2000. Aquatic Feeding in Salamanders. In: Schwenk, K. (Ed.): *Feeding. Form, Function, and Evolution in Tetrapod Vertebrates*, pp. 65–94. Academic Press, Boston.

Dohrn, A. 1884. Studien zur Urgeschichte des Wirbeltierkörpers. IV. Die Entwicklung und Differenzierung der Kiemenbögen der Selachier. – *Mitteilungen der Zoologischen Station Neapel* **5**: 102–151.

Downs, J. P., Daeschler, E. B., Jenkins, F. A. and Shubin, N. H. 2008. The cranial endoskeleton of *Tiktaalik roseae*. – *Nature* **455**: 925–929.

Drüner, L. 1902. Studien zur Anatomie der Zungenbein-, Kiemenbogen- und Kehlkopfmuskeln der Urodelen. Theil 1. – *Zoologische Jahrbücher für Anatomie* **15**: 435–622.

Drüner, L. 1904. Studien zur Anatomie der Zungenbein-, Kiemenbogen- und Kehlkopfmuskeln der Urodelen. Theil 2. – *Zoologische Jahrbücher für Anatomie* **17**: 361–690.

Duellman, W. E. and Trueb, L. 1986. *Biology of Amphibians*. Johns Hopkins, Baltimore.

Ericsson, R., Joss, J. and Olsson, L. 2008. The fate of cranial neural crest cells in the Australian lungfish, *Neoceratodus forsteri*. – *Journal of Experimental Zoology B, Molecular and Developmental Evolution* **310B**: 345–354.

Forey, P. L. 1998. *History of the Coelacanth Fishes*. Chapman and Hall, London.

Forey, P. L., Gardiner, B. G. and Patterson, C. 1991. The lungfish, the coelacanth, and the cow revisited. In: Schultze, H. P. and Trueb, L. (Eds): *Origins of the Higher Groups of Tetrapods*, pp. 145–172. Cornell University Press, Ithaca.

Fritzsch, B. 1987. Inner ear of the coelacanth fish *Latimeria* has tetrapod affinities. – *Nature* **327**: 153–154.

Gans, C. 1970. Respiration in early tetrapods: the frog is a red herring. – *Evolution* **24**: 723–734.

Gegenbaur, C. 1901. *Vergleichende Anatomie der Wirbeltiere*, volume 2. Engelmann, Leipzig.

Godfrey, S. J. 2003. A diminutive temnospondyl amphibian from the Pennsylvanian of Illinois. – *Canadian Journal of Earth Sciences* **40**: 507–514.

Goette, A. 1901. Über die Kiemen der Fische. – *Zeitschrift für wissenschaftliche Zoologie* **69**: 533–577.

Goodrich, E. S. 1930. *Studies on the Structure and Development of Vertebrates*. Chicago University Press, Chicago.

Greil, A. 1906. Über die Homologie der Anamnierkiemen. – *Anatomischer Anzeiger* **28**: 257–272.

Hellrung, H. 2003. *Gerrothorax pustuloglomeratus*, ein Temnospondyle (Amphibia) mit knöcherner Branchialkammer aus dem Unteren Keuper von Kupferzell (Süddeutschland). – *Stuttgarter Beiträge zur Naturkunde B* **330**: 1–130.

Hermens, M., Daffé, M. and Vandewalle, P. 2007. Observations of the reduction of external gill filaments during larval development in *Heterotis niloticus*. – *Belgian Journal of Zoology* **137**: 247–249.

Hotker, J. 1926. *Archegosaurus Decheni* Goldfuss. Untersuchung des Schädelbaues. – *Palaeontologia Hungarica* **2**: 109–130.

Hook, R. W. 1983. *Colosteus scutellatus* (Newberry), a primitive temnospondyl amphibian from the Middle Pennsylvanian of Linton, Ohio. – *American Museum Novitates* **2770**: 1–41.

Ivakhnenko, N. 1981. Discosauriscidae from the Permian of Tadzhikistan. – *Paleontological Journal* **1981**: 90–102.

Ivakhnenko, N. 1987. Permian parareptiles of the Soviet Union. – *Trudy Paleontologicheskogo Instituta SSSR* **223**: 1–158.

Janis, C. M. and Keller, J. C. 2001. Modes of ventilation in early tetrapods: costal aspiration as a key feature of amniotes. – *Acta Palaeontologica Polonica* **46**: 137–170.

Janvier, P. 1996. *Early Vertebrates*. Oxford University Press, Oxford.

Jarvik, E. 1980. *Basic Structure and Evolution of Vertebrates*, volume 1. Academic Press, London.

Klembara, J. 1995. The external gills and ornamentation of skull-roof bones of the lower Permian *Discosauriscus* (Kuhn 1933) with remarks to its ontogeny. – *Paläontologische Zeitschrift* **69**: 265–281.

Klembara, J. and Ruta, M. 2004. The seymouriamorph tetrapod *Utegenia shpinari* from the Upper Carboniferous-Lower Permian of Kazakhstan. Part I: cranial anatomy and ontogeny. – *Transactions of the Royal Society of Edinburgh, Earth Sciences* **94**: 45–74.

Klembara, J. and Ruta, M. 2005. The seymouriamorph tetrapod *Ariekanerpeton sigaleni* from the Lower Permian of Tadzhikistan. Part I: cranial anatomy and ontogeny. – *Transactions of the Royal Society of Edinburgh, Earth Sciences* **96**: 43–70.

Lauder, G. V. and Wainwright, P. C. 1992. Function and history: the pharyngeal jaw apparatus in primitive ray-finned fishes. In: Mayden, R. L. (Ed.): *Systematics, Historical Ecology, and North American Freshwater Fishes*, pp. 455–471. Stanford University Press, Palo Alto.

Laurin, M. and Reisz, R. R. 1997. A new perspective on tetrapod phylogeny. In: Sumida, S. S. and Martin, K. L. M. (Eds): *Amniote Origins: Completing the Transition to Land*, pp. 9–59. Academic Press, London.

Lebedev, O. A. and Coates, M. I. 1995. The postcranial skeleton of the Devonian tetrapod *Tulerpeton curtum* Lebedev. – *Zoological Journal of the Linnean Society* **114**: 307–348.

Lombard, R. E. and Bolt, J. R. 1995. A new primitive tetrapod, *Whatcheeria deltae*, from the Lower Carboniferous of Iowa. – *Palaeontology* **38**: 471–494.

Mallat, J. 1984. Early vertebrate evolution: pharyngeal structure and the origin of gnathostomes. – *Journal of Zoology* **204**: 169–183.

Meyer, H.v. 1858. Reptilien aus der Steinkohlenformation in Deutschland. – *Palaeontographica* **6**: 59–219.

Meyer, A. and Wilson, A. C. 1990. Origin of tetrapods inferred from their mitochondrial DNA affiliation to lungfish. – *Journal of Molecular Evolution* **31**: 359–364.

Milner, A. R. 1982. Small temnospondyl amphibians from the Middle Pennsylvanian of Illinois. – *Palaeontology* **25**: 635–664.

Milner, A. C. and Lindsay, W. 1998. Postcranial remains of *Baphetes* and their bearing on the relationships of the Baphetidae (= Loxommatidae). – *Zoological Journal of the Linnean Society* **122**: 211–235.

Milner, A. C., Milner, A. R. and Walsh, S. A. 2009. A new specimen of *Baphetes* from Nýřany, Czech Republic and the intrinsic relationships of the Baphetidae. – *Acta Zoologica (Stockholm)* **90**(special issue): 318–334.

Moroff, T. 1904. Über die Entwicklung der Kiemen bei Fischen. – *Archiv für mikroskopische Anatomie* **64**: 189–213.

Nilsson, T. 1946. A new find of *Gerrothorax rhaeticus* Nilsson, a plagiosaurid from the Rhaetic of Scania. – *Acta Universitatis Lundensis* **42**: 1–42.

Noble, G. K. 1931. *The biology of the Amphibia*. McGraw Hill, New York.

Olson, E. C. 1979. Aspects of the biology of *Trimerorhachis* (Amphibia: Temnospondyli). – *Journal of Paleontology* **53**: 1–17.

Packard, G. C. 1976. Devonian amphibians: did they excrete carbon dioxide via skin, gills, or lungs?. – *Evolution* **30**: 270–280.

Pelpster, B. and Bemis, W. E. 1992. Structure and function of the external gill filaments of embryonic skates (*Raja erinacea*). – *Respiration Physiology* **89**: 1–13.

Perry, S. F. and Sander, P. M. 2004. Reconstructing the evolution of the respiratory apparatus in tetrapods. – *Respiration Physiology and Neurobiology* **144**: 125–139.

Rauther, M. 1937. Kiemen der Anamnier, Kiemendarmderivate der Cyclostomen und Fische. In: Bolk, L., Göppert, E., Kallius, E. and Lubosch, W. (Eds): *Handbuch der vergleichenden Anatomie der Wirbeltiere*, volume 3, pp. 211–278. Urban and Schwarzenberg, Berlin.

Rauther, M. 1940. Das Kiemensystem. In Bronn, H. G. (Ed.): *Klassen und Ordnungen des Tierreichs*, volume 6, pp. 711–758. Akademische Verlagsgesellschaft, Leipzig.

Reilly, S. M. and Lauder, G. V. 1988. Atavisms and the homology of hyobranchial elements in lower vertebrates. – *Journal of Morphology* **195**: 237–245.

Romer, A. S. 1958. Tetrapod limbs and early tetrapod life. – *Evolution* **12**: 365–369.

Romer, A. S. 1972. Skin breathing – primary or secondary?. – *Respiration Physiology* **14**: 183–192.

Rose, C. S. 2003. The developmental morphology of salamander skulls. In: Heatwole, H. (Ed.): *Amphibian Biology*, volume 5: *Osteology*, pp. 1684–1781. Surrey Beattey, Chipping Norton.

Ruta, M. and Coates, M. I. 2007. Dates, nodes and character conflict: addressing the lissamphibian origin problem. – *Journal of Systematic Palaeontology* **5**: 69–122.

Schmalhausen, I. I. 1955. The gills and gill septa of Amphibia. – *Zoologicheskij Zhurnal* **34**: 383–398. [In Russian]

Schmalhausen, I. I. 1968. *The origin of terrestrial vertebrates*. Academic Press, New York.

Schoch, R. R. 1999. Studies on braincases of early tetrapods: structure, morphological diversity, and phylogeny – 1. Trimerorhachis and other primitive temnospondyls. – *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **213**: 233–259.

Schoch, R. R. 2001. Can metamorphosis be recognized in Palaeozoic amphibians?. – *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **221**: 335–367.

Schoch, R. R. 2006. A complete trematosaurid amphibian from the Middle Triassic of Germany. – *Journal of Vertebrate Paleontology* **26**: 29–43.

Schoch, R. R. 2008. A new stereospondyl from the Middle Triassic of Germany, and the origin of the Metoposauridae. – *Zoological Journal of the Linnean Society* **152**: 79–113.

Schoch, R. R. 2009. The evolution of life cycles in early amphibians. – *Annual Review of Earth and Planetary Sciences* **37**: 135–162.

Schoch, R. R. and Witzmann, F. 2009. The temnospondyl *Glanochthon* from the Permian Meisenheim Formation of Germany. – *Special Papers in Palaeontology* **81**: 121–136.

Schultze, H.-P. 1984. Juvenile specimens of *Eusthenopteron foordi* Whiteaves from the Late Devonian of Miguasha, Quebec, Canada. – *Journal of Vertebrate Paleontology* 4: 1–16.

Schultze, H.-P. 1991. A comparison of controversial hypotheses on the origin of tetrapods. In: Schultze, H.-P. and Trueb, L. (Eds): *Origins of the Higher Groups of Tetrapods*, pp. 145–172. Cornell University Press, Ithaca.

Sewertzoff, A. N. 1924. Die Entwicklung der Kiemen und Kiemengefässe bei Fischen. – *Zeitschrift für wissenschaftliche Zoologie* **121**: 494–556.

Shishkin, M. A. 1987. Evolution of early amphibians (Plagiosauroidea). – *Trudy Paleontologicheskogo Instituta* **225**: 1–143. [In Russian].

Sollas, W. J. 1920. On the structure of *Lysorophus*, as exposed by serial sections. – *Philosophical Transactions of the Royal Society B* **209**: 481–527.

Starck, D. 1982. *Vergleichende Anatomie der Wirbeltiere auf evolutionsbiologischer Grundlage*, volume 3. Springer, Heidelberg.

Steen, M. 1937. On *Acanthostoma vorax* Credner. – *Proceedings of the Zoological Society London B* **107**: 491–500.

Sushkin, P. 1936. Notes on the pre-Jurassic tetrapoda from USSR. 3. Dvinosaurus amalitzky, a perennibranchiate stegocephalian from the Upper Permian from North Dvina. – *Trudy Paleontologichesko Instituta Nauka SSSR* 4: 43–91.

Van Hoepen, E. C. N. 1915. Stegocephalia of Senekal. – *Annals of the Transvaal Museum Orange Free State* **5**: 124–149.

Wake, D. B. 1966. Comparative osteology of the lungless salamanders, Family Plethodontidae. – *Memoirs of the Southern California Academy of Sciences* 4: 1–111.

Warren, A. and Marsicano, C. 1998. Revision of the Brachyopidae (Temnospondyli) from the Triassic of Sydney, Carnarvon and Tasmania Basins, Australia. – *Alcheringa* **22**: 329–342.

Watson, D. M. S. 1956. The brachyopid labyrinthodonts. – *Bulletin of the British Museum (Natural History). Geology Series* **2**: 315–392.

Werneburg, R. 1988. Die Stegocephalen (Amphibia) der Goldlauterer Schichten (Unterrotliegendes, Perm) des Thüringer Waldes. Teil III: Apateon dracyiensis (Boy), Branchierpeton reinholdi n. sp. und andere. – *Veröffentlichungen des Naturkundemuseums Erfurt* 7: 80–96.

Werneburg, R. 1991. Die Branchiosaurier aus dem Unterrotliegend des Döhlener Beckens bei Dresden. – *Veröffentlichungen des Naturhistorischen Museums Schleusingen* **6**: 75–99.

Werneburg, R. 1998. Ein larvaler *Acanthostomatops* (Zatrachydidae, Amphibia) aus der Niederhäslich-Formation (Unter-Perm) des Döhlen-Beckens. – *Veröffentlichungen des Museums für Naturkunde Chemnitz* **21**: 49–52.

Werneburg, R. 2002. *Apateon dracyiensis* – eine frühe Pionierform der Branchiosaurier aus dem Europäischen Rotliegend. Teil 2: Paläoökologie. – *Veröffentlichungen Naturhistorisches Museum Schleusingen* **17**: 17–32.

Werneburg, R. 2009. The Permotriassic branchiosaurid *Tungussogyrinus* Efremov, 1939 (Temnospondyli, Dissorophoidea) from Siberia restudied. – *Fossil Record* **12**: 105–120.

Wilder, I. W. 1925. *The Morphology of Amphibian Metamorphosis*. Smith College 50th anniversary Publication, Northampton.

Witzmann, F. 2004. The external gills of Palaeozoic amphibians. – *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **232**: 375–401.

Witzmann, F. 2005. Hyobranchial and postcranial ontogeny of the temnospondyl *Onchiodon labyrinthicus* (Geinitz, 1861) from Niederhäslich (Döhlen Basin, Autunian, Saxony). – *Paläontologische Zeitschrift* **79**: 479–492.

Witzmann, F. 2006. Morphology and palaeobiology of the Permo-Carboniferous temnospondyl amphibian *Archegosaurus decheni* Goldfuss, 1847 from the Saar-Nahe Basin, Germany. – *Transactions of the Royal Society of Edinburgh Earth Sciences* **96**: 131–162.

Witzmann, F. 2007. The evolution of the scalation pattern in temnospondyl amphibians. – *Zoological Journal of the Linnean Society* **150**: 815–834.

Witzmann, F. and Pfretzschner, H.-U. 2003. Larval ontogeny of Micromelerpeton credneri (Temnospondyli, Dissorophoidea). – *Journal of Vertebrate Paleontology* **150**: 815–834.

Witzmann, F. and Schoch, R. R. 2006a. The postcranium of *Archegosaurus decheni*, and a phylogenetic analysis of temnospondyl postcrania. – *Palaeontology* **49**: 1211–1235.

Witzmann, F. and Schoch, R. R. 2006b. Skeletal development of the temnospondyl *Acanthostomatops vorax* from the Lower Permian Döhlen Basin of Saxony. – *Transactions Royal Society Edinburgh* **96**: 365–385.

The hyobranchial apparatus in early tetrapods and its significance for feeding and breathing

Appendix 12

Witzmann, F. & Schoch, R. R. 2013. Reconstruction of cranial and hyobranchial muscles in the Triassic temnospondyl *Gerrothorax* provides evidence for akinetic suction feeding. – Journal of Morphology 274: 525–542.

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Reconstruction of Cranial and Hyobranchial Muscles in the Triassic Temnospondyl *Gerrothorax* Provides Evidence for Akinetic Suction Feeding

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ABSTRACT The cranial and hyobranchial muscles of the Triassic temnospondyl *Gerrothorax* have been reconstructed based on direct evidence (spatial limitations, ossified muscle insertion sites on skull, mandible, and hyobranchium) and on phylogenetic reasoning (with extant basal actinopterygians and caudates as bracketing taxa). The skeletal and soft-anatomical data allow the reconstruction of the feeding strike of this bottom-dwelling, aquatic temnospondyl. The orientation of the muscle scars on the postglenoid area of the mandible indicates that the depressor mandibulae was indeed used for lowering the mandible and not to raise the skull as supposed previously and implies that the skull including the mandible must have been lifted off the ground during prey capture. It can thus be assumed that *Gerrothorax* raised the head toward the prey with the jaws still closed. Analogous to the bracketing taxa, subsequent mouth opening was caused by action of the strong epaxial muscles (further elevation of the head) and the depressor mandibulae and rectus cervicis (lowering of the mandible). During mouth opening, the action of the rectus cervicis muscle also rotated the hyobranchial apparatus ventrally and caudally, thus expanding the buccal cavity and causing the inflow of water with the prey through the mouth opening. The strongly developed depressor mandibulae and rectus cervicis, and the well ossified, large quadrate-articular joint suggest that this action occurred rapidly and that powerful suction was generated. Also, the jaw adductors were well developed and enabled a rapid mouth closure. In contrast to extant caudate larvae and most extant actinopterygians (teleosts), no cranial kinesis was possible in the *Gerrothorax* skull, and therefore suction feeding was not as elaborate as in these extant forms. This reconstruction may guide future studies of feeding in extinct aquatic tetrapods with ossified hyobranchial apparatus. J. Morphol. 274:525–542, 2013.

KEY WORDS: aquatic tetrapods; extant phylogenetic bracket; muscle reconstruction; Plagiosauridae

INTRODUCTION

Vertebrate fossils often provide a rich source of anatomical information, permitting the reconstruction of soft tissues in adjacent regions of preserved bones. Important data are yielded by the attachment of musculature, which is preserved in some detail in a range of groups. To use these data correctly, muscle attachments of extant taxa need to be studied and the observations inferred on the extinct taxon by means of phylogenetic reasoning, the so-called extant phylogenetic bracket (EPG; Witmer, 1995). An outstanding example is the Triassic temnospondyls, probably distant relatives of lissamphibians that reached sizes in the range of 2–5 m. In such large forms, muscle attachments and other correlates of soft-tissue features are more readily identified and distinguished than in small taxa. Triassic temnospondyls are known from several fossil deposits with excellent preservation, preserving bone surface structures in great detail. Here, we focus on the rich material of the plagiosaurid *Gerrothorax pulcherrimus* (Fraas, 1913) from Kupferzell, in which traces of muscle attachments can be identified and compared in depth to extant taxa.

The Early to Late Triassic plagiosaurids are a group of fully aquatic, gill-breathing temnospondyls that inhabited a wide range of environments from shallow marine to freshwater lakes and streams. Characteristic are the broad, short-snouted skulls with large orbits and a generally flattened morphology of skull and postcranium (Fig. 1A; Warren, 2000; Damiani et al., 2009). For a long time, the phylogenetic position of plagiosaurids within temnospondyls had formed a matter of debate, but recent phylogenetic analyses (Yates and Warren, 2000; see also Schoch, 2008; Schoch, in press) suggest plagiosaurids to be closely related to the Trematosauria

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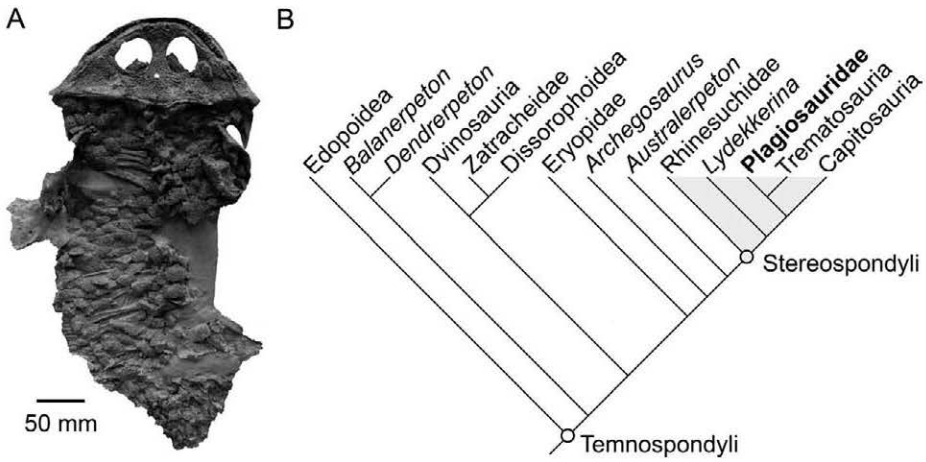

Fig. 1. (**A**) Almost complete, articulated skeleton of *Gerrothorax pulcherrimus* (SMNS 83866). (**B**) Phylogenetic position of the Plagiosauridae within the Temnospondyli. Cladogram simplified from Schoch (in press).

among stereospondyls (Fig. 1B). Several new findings of this group of temnospondyls have attracted the interest of many paleontologists in recent years (Hellrung, 2003; Jenkins et al., 2008; Damiani et al., 2009; Dias-da-Silva and Milner, 2010; Witzmann et al., 2012; Schoch and Witzmann, 2012). Among plagiosaurids, *Gerrothorax* is the by far best-known genus, which is known from abundant cranial and postcranial material from Middle and Late Triassic strata of Greenland, Sweden, and Germany. The high degree of ossification of the endochondral skull (Witzmann et al., 2012) and pachyostosis (i.e., the cortex of the bone is much thickened and dense; Castanet et al., 2003) in the postcranial skeleton together with the complete coverage of the trunk by thick osteoderms (Nilsson, 1946a; Hellrung, 2003; Witzmann and Soler-Gijón, 2010; Witzmann, 2011) increased the weight of *Gerrothorax* considerably and strongly suggest a bottom dwelling mode of life.

Although these data provide compelling evidence for the life habits of *Gerrothorax*, the question how this aberrant aquatic tetrapod fed remains controversial and essentially unanswered (Panchen, 1959; Hellrung, 2003; Jenkins et al., 2008). This applies especially for the extensively ossified hyobranchial apparatus of *Gerrothorax*, whose functional role during prey capture has so far been largely neglected. The objective of this study is therefore to achieve a comprehensive understanding of the feeding apparatus in this fully aquatic tetrapod. In the first step, using an EPG, skeletal correlates of soft tissues will be used as guide to reconstruct cranial and hyobranchial muscles. In addition to these correlates (e.g., muscle scars), facets of well-preserved hyobranchial elements provide further information. In the second step, an integrated functional hypothesis of prey capture in *Gerrothorax* will be developed on the existing platform of skeletal and soft-anatomical data.

MATERIALS AND METHODS

We follow the conclusion of Jenkins et al. (2008) and Schoch and Witzmann (2012) that *Gerrothorax* is monospecific with *G. pulcherrimus* (Fraas, 1913) as the only valid species. The following specimens of *G. pulcherrimus* were investigated for this study: From the Middle Triassic of southern Germany (Kupferzell and Vellberg): SMNS 83070, parts of skull and lower jaw; 83382, isolated ceratobranchial; 83866, articulated skeleton with almost completely preserved hyobranchial apparatus; 84786, disarticulated skeleton including almost complete, three-dimensionally preserved skull; 84787, posterior portion of skull table and palate including the subtemporal fenestra and complete lower jaw; 84788, posterior portion of skull including occiput and neurocranium; 84791, lower jaw; 91354, anterior part of skull with interorbital region and lower jaw; SMNS uncatalogued, posterior part of lower jaw with adductor fossa and postglenoid area. From the Late Triassic of Greenland: MGUH 28919, skull and almost complete hyobranchium in ventral view. From the Late Triassic of Sweden: NRM-PZ B.18, fragments of skull, hyobranchium, and postcranial skeleton.

The reconstruction of musculature in fossil vertebrates requires a four-step approach that uses the EPB (Fig. 2). (1) Spatial limitations serve as a first approximation to guide the search for muscle arrangement and assessment of maximal volumes of soft tissue. The closed skull of *Gerrothorax* makes such a procedure much easier than the fenestrate skulls of lissamphibians and most amniotes. This is one of the reasons why basal actinopterygians (*Polypterus*, *Amia*) are better suited as outgroups than the highly derived and fenestrate actinistians and dipnoans (Lauder, 1980; Janvier, 1996; see below). (2) Skeletal correlates of muscles (sites of attachment for muscle fibers and tendons, "muscle scars") are then studied, guided by first-hand

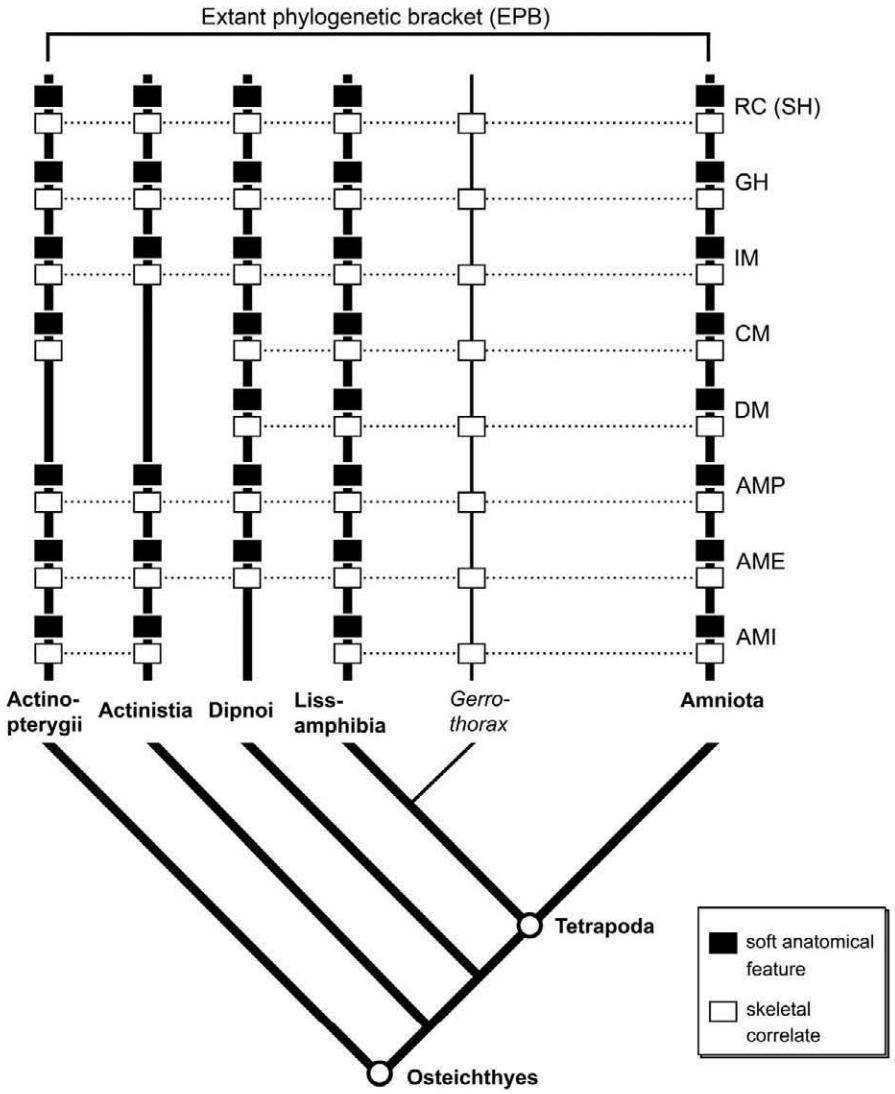

Fig. 2. Extant phylogenetic bracket (EPB) from which the presence of certain muscles in *Gerrothorax* is hypothesized. Data for the presence of muscles in extant forms were taken mainly from Allis (1897, 1922), Luther (1914), Lubosch (1938), Säve-Söderbergh (1945), Fox (1954), Carroll and Holmes (1980), Lauder (1980), Bemis (1986), Bemis and Lauder (1986), Iordanskij (1990), Elwood and Cundall (1994), Bauer (1997), and Diogo et al. (2008a, b). Bold: extant taxa. AME, adductor mandibular externus; AMI, adductor mandibulae internus; AMP, adductor mandibulae posterior; CM, cleidomastoideus; DM, depressor mandibulae; GH, geniohyoideus (corresponds to the coracomandibularis in osteichthyan fishes); IM, intermandibularis (it is not distinguished between intermandibularis anterior and posterior here); RC, rectus cervicis; SH, sternohyoideus.

examination of such correlates in extant samples. (3) In this step, the EPB procedure is applied. The presence of a given muscle in bracket taxa (e.g., actinopterygians and caudates) indicates that a homolog of this muscle might have been present in the fossil taxon. (4) Finally, skeletal correlates ("muscle scars") are sought to confirm this hypothesis. In the case of

absence of correlates the hypothesis is not falsified, but simply less well-supported. Likewise, when a given muscle is present in only one of the bracket taxa, the inference is less robust. Another point to be considered is individual variation: more often than not are soft-tissue correlates present in one specimen and absent in another one, or even vary between left and right sides of the same skull.

In *Gerrothorax*, attachment sites for muscles and tendons (rugosities, ridges, grooves, bosses etc.) are often preserved on the internal (ventral) surface of the skull roofing bones, the palate, and the area of the adductor fossa and postglenoid area (retroarticular process) of the mandible. These ossified structures may even allow the reconstruction of muscle fiber orientations. In basal tetrapods, the skull is usually heavily ossified with the skull roof being closed except for the orbits, the nostrils and the parietal opening, and the subtemporal fossa of the palate and the adductor fossa of the mandible are well defined. Thus, the extent of the jaw muscles is limited by rigid bony walls and the height of the skull, giving a rough impression of the size of their particular parts.

The basal actinopterygians *Polypterus*, *Amia* and *Lepisosteus*, dipnoans, and extant caudates were chosen as extant bracketing taxa. Data for cranial and hyobranchial muscles in basal actinopterygians were taken from Allis (1897, 1922) and Lauder (1980), for extant dipnoans from Bemis (1986) and Bemis and Lauder (1986), and for extant amphibians from Drüner (1901, 1904), Luther (1914), Lubosch (1938), Säve-Söderbergh (1945), Fox (1954), Jarvik (1963), Carroll and Holmes (1980), Iordanskij (1990), Bauer (1997), Haas (2001), and Johnston (2011). The works of Edgeworth (1935), Wiley (1979), and Diogo et al. (2008a,b) provide more general accounts on cranial and hyobranchial muscles and their homologies in vertebrates. Admittedly, a general problem is the fact that homologies between the cranial muscles in different groups of vertebrates (in our case osteichthyan fishes and lissamphibians) are often not well established and deserve future studies in morphology, embryology, and molecular genetics.

The EPB method permits the inference of muscles or muscle portions in extinct taxa, provided that muscle scars are identified in the fossil material. To permit this inference, these muscle scars need to be found in the same place in the bracketed taxa and the fossil taxon, that is, fulfill the topographical homology criterion. These skeletal correlates are then interpreted within the frame of an existing phylogenetic hypothesis, which means that they are effectively mapped onto that preexisting cladogram. However, inferred soft tissues cannot contribute to build phylogenetic hypotheses by themselves. Therefore, apomorphic or plesiomorphic conditions of inferred soft tissues cannot be recognized, other than slight variations in the attachment sites per se.

Temnospondyls, "anthracosaurs" and lepospondyls are treated here as crown-group tetrapods (e.g., Ruta and Coates, 2007; for a different view see Marjanović and Laurin, 2008) and are named "basal tetrapods" in this study. The term "crown-group tetrapod" is used here in the sense of Hennig (1966) as encompassing the last common ancestor of all living tetrapods and all of its descendants, both extinct and extant. The stem-group tetrapods define all fossil taxa that are more closely related to crown-group tetrapods than to the extant group that is the closest relative of the crown-group tetrapods [either actinistians (e.g., Zhu and Schultze, 2001) or dipnoans (e.g., Cloutier and Ahlberg, 1996)].

INSTITUTIONAL ABBREVIATIONS: MGUH, Geological Museum, University of Copenhagen, Denmark; NRM, Naturhistoriska riksmuseet Stockholm, Sweden; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany.

RESULTS

Muscle Attachment Sites on the Ventral Side of the Skull Roof

Os squamosum. On the posteromedial portion of the squamosal bone, anterior to the descending lamina, are closely spaced, conspicuous striae that are aligned posteromedially, anteroposteriorly and posterolaterally and attain a reticulate appearance in the vicinity to the squamosal-pterygoid suture of SMNS 84787 (Fig. 3). More anteriorly is a large pit with an appertaining, short furrow that is directed anteromedially. In SMNS 84786, the scars anterior to the descending lamina are likewise distinct but are mainly arranged anterolaterally. There is a second pit in this specimen, located anterolateral to the attachment site and the appertaining furrow is directed laterally (Fig. 4A,B).

Os quadratojugale. In SMNS 84787 (Fig. 3) and 84786 (Fig. 4A,B), scars are present on the quadratojugal bone that are aligned parallel to the lateral skull margin and extend anteriorly toward the jugal, where they may continue. Three pits can be found in the posterolateral corner of the quadratojugal bone in SMNS 84788.

Os jugale. The ventral surface of the jugal bone in SMNS 84787 (Fig. 3) and 84786 (Fig. 4A,B) is rugose and possesses posteromedially and anteroposteriorly directed striae in its posterior part that may extend toward the quadratojugal (see above). In the latter specimen, also the anterior and central portions of the bone are visible that bear numerous large pits.

Os parietale and os frontale. The parietal bone bears a distinctly roughened surface consisting of fine ridges and furrows anterior to the level of the anterior margin of the basal plate (SMNS 84787; Fig. 3). The ridges and furrows are mainly aligned anteriorly and anteromedially. Anterior to this site is located a large pit. Rugosities on the parietal bone can also be observed in SMNS 91354, where they extend onto the frontal bone. Due to poor preservation, it cannot be ascertained if the attachment sites on parietal bone and frontal bone extended on the lateral sides of epipterygoid and sphenethmoid bones.

Orbital margin. In certain temnospondyls and other basal tetrapods, parts of the orbital rim were interpreted as attachment sites of adductor muscles (e.g., Beaumont, 1977; Damiani et al., 2009). In *Gerrothorax*, however, this was not possible because the dermal sculpture of the external bone surface extends directly on the edge of the orbital margin and even continues on the ventral surface of postfrontal and frontal bones (Fig. 3). Dermal sculpture in basal tetrapods indicates that the bone surface was directly overlain by integument in the living animal (Witzmann et al., 2010), and attachment of muscles can be ruled out in this area.

Muscle Attachment Sites on the Palate and the Quadrate

Os pterygoideus. The lateral margin of the palatine ramus of the pterygoid bone in SMNS

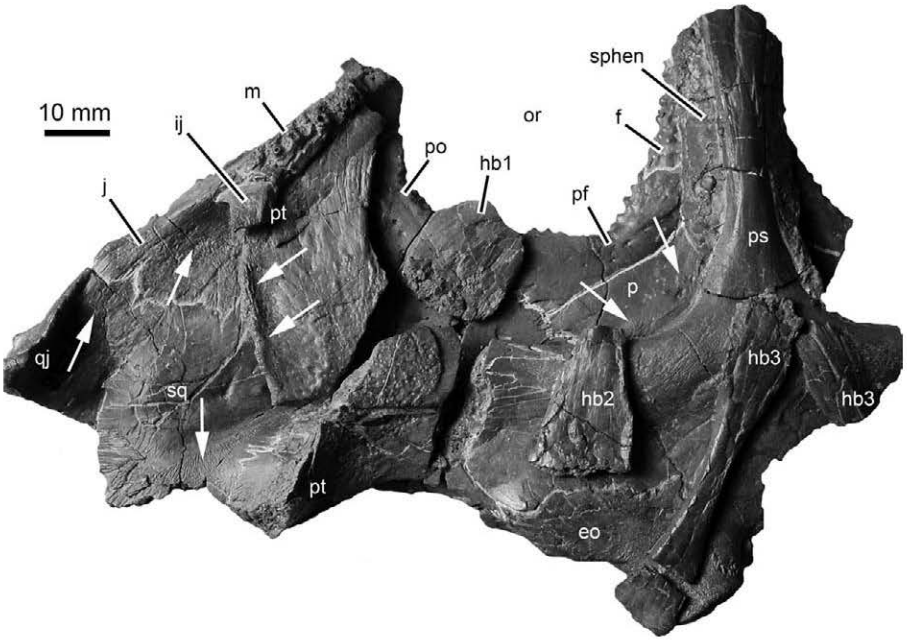

Fig. 3. Ossified structures interpreted as muscle attachment sites (marked by arrows) in *Gerrothorax pulcherrimus*. SMNS 84787, posterior part of skull roof and palate in ventral view. eo, exoccipital; f, frontal; hb, hypobranchial; ij, insula jugalis; j, jugal; m, maxilla; or, orbit; p, parietal; pf, postfrontal; po, postorbital; ps, parasphenoid; pt, pterygoid; qj, quadratojugal; sphen, spheneth-moid; sq, squamosal.

84787 and 84788 bears distinct parallel striae that may terminate in spike-like projections (Fig. 3). The striae and projections are directed mainly laterally. In both specimens, it is well visible that the lateral margin of the palatine ramus is downturned, and that the striae extend onto the dorsal side of the bone (Fig. 4C,D).

Os quadratum. The quadrate bone bears four large, longitudinally arranged ridges anterior to the quadrate trochlea (Fig. 4E,F). They are directed anterodorsally toward the ventral surface of the squamosal bone.

Muscle Attachment Sites on the Occipital Region

Os postparietale and os tabulare. The occipital lamellae of the postparietal bones extend posteroventrally to contact the exoccipital bones. They are not sculptured but possess numerous tuberosities. The occipital lamellae of the tabular bones are likewise unsculptured and have a roughened surface.

Os squamosum. The occipital face of the squamosal bone bears a prominent, raised area of ovate outline, and a distinctly concave surface (Fig. 4G). The dorsal rim of this area is rugose, whereas the remaining surface bears faint striae.

Os quadratojugale. The occipital face of the quadratojugal bone extends far ventrally to contact the quadrate bone. It is posteriorly distinctly concave and has a large paraquadrate foramen in its dorsolateral part (Witzmann et al., 2012). Broad, radially aligned depressions are visible ventral and ventromedial to this foramen (Fig. 4G).

Os quadratum. The deep posterior face of the quadrate that wedges between the descending laminae of squamosal and quadratojugal dorsally and between the quadrate ramus of pterygoid and the descending lamina of squamosal dorsomedially has fine radial striae in its dorsal portion (Fig. 4G).

Os exoccipitale. Distinct tuberosities can be observed on the vertical column and the paroccipital process of the exoccipital (Fig. 4H).

Muscle Attachment Sites on Lower Jaw

Processus preglenoidalis. The prearticular bone forms the prominent, medially directed preglenoid process on the posteromedial side of the

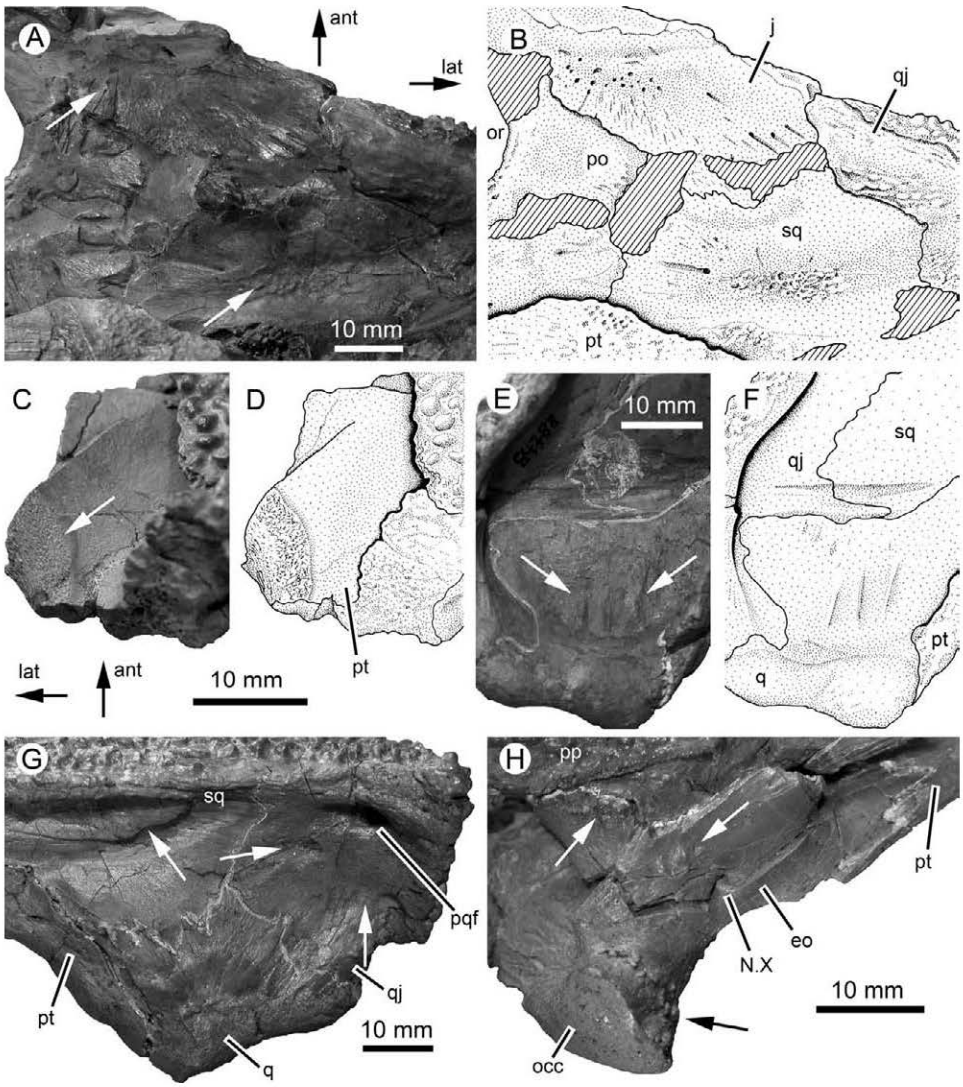

Fig. 4. Ossified structures interpreted as muscle attachment sites (marked by arrows) in *Gerrothorax pulcherrimus*. (**A**) SMNS 84786, region of left "cheek" posterolateral to the orbit in ventral view. (**B**) Interpretative drawing of A. (**C**) SMNS 84787, lateral margin of left pterygoid in dorsal view. (**D**) Interpretative drawing of C. (**E**) SMNS 84788, right quadrate in anteroventral view. (**F**) Interpretative drawing of E. (**G**) SMNS 84788, occipital view of right squamosal, quadratojugal and quadrate. (**H**) SMNS 84788, right occipital condyle of exoccipital in dorsal view. ant, anterior; eo, exoccipital; j, jugal; lat, lateral; N.X, opening for vagus nerve; occ, occipital condyle; or, orbit; po, postorbital; pp, postparietal; pqf, paraquadrate foramen; pt, pterygoid; q, quadrate; qj, quadratojugal; sq, squamosal.

adductor chamber (Fig. 5A,B). This process is dorsally concave and may bear muscle scars on its dorsal and ventral side. In specimen SMNS 84787, anteromedially and dorsally aligned striae are well discernable on the dorsolateral portion of the preglenoid process.

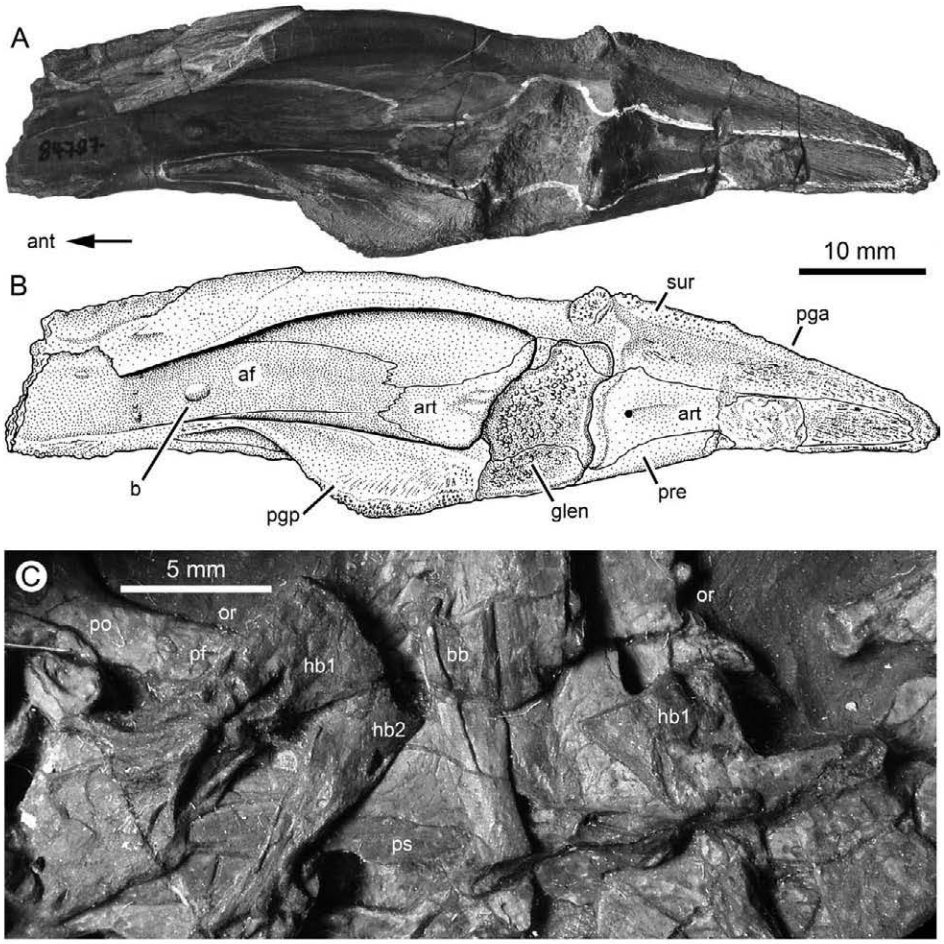

Fig. 5. Ossified structures interpreted as muscle attachment sites in *Gerrothorax pulcherrimus*. (**A**) SMNS 84787, posterior portion of right mandibular ramus (adductor fossa, glenoid and postglenoid area) in dorsal view. (**B**) Interpretative drawing of A. (**C**) MGUH 28919, anteroventral hyobranchial elements (basibranchial and hypobranchials) in ventral view. af, adductor fossa; ant, anterior; art, articular; b, boss on the floor of adductor fossa; bb, basibranchial; glen, glenoid; hb, hypobranchial; or, orbit; pf, postfrontal; pga, postglenoid area; pgp, preglenoid process; po, postorbital; pre, prearticular; ps, parasphenoid; sur, surangular.

Adductor chamber. On the anterior portion of the floor of adductor chamber is located a large, anteroposteriorly elongate boss (Fig. 5A,B).

Postglenoid area. The postglenoid area or retroarticular process is large in *Gerrothorax* and its length accounts for more than one sixth of that of the mandible. According to Hellrung (2003), the dorsal surface of the postglenoid area is mostly formed by the surangular bone laterally and the articular bone medial to it; the medial part of the dorsal surface is formed by a narrow portion of the prearticular. The surangular bone forms a deep, anteroposteriorly elongate trough. In SMNS 84787, anteroposteriorly aligned muscle scars are well visible in this trough (Fig. 5A,B). Medial to this prominent depression is a distinct foramen on the articular a short distance posterior to the glenoid. This foramen is located in a shallowly concave area.

Symphysis, coronoid, and splenial series. The mandibular symphysis in SMNS 84791 is

posteriorly concave and bears distinct tuberosities. The bone surface of the coronoids ventral to the raised denticulated areas shows rugosities with mainly anteromedially directed striae (best visible in SMNS 83797). The series of splenial bones shows no muscle scars but is clearly concave medially and a conspicuous furrow is visible ventrally from the region of the postglenoid area until to the height of the midpart of coronoid 2 in SMNS 84791.

Further Cranial Characters Related to Cranial Musculature and Feeding

Insula jugalis. This structure is a ventral outgrowth of the jugal bone and articulates with the maxilla laterally and anterolaterally, the ectopterygoid bone medially and anteromedially, and the pterygoid bone medially (Fig. 3). Its posterior, broadly rounded edge forms the pointed anterior margin of the subtemporal fenestra and has the morphology of a trochlea.

Mandibular joint. The trochlea of the well-ossified quadrate bone and the glenoid facet of the lower jaw consist of unfinished bone, i.e., they have a roughened surface that was covered by cartilage in life. The unusually large quadrate trochlea is screw-shaped and consists of a larger median and a smaller lateral spindle (Fig. 4E,F). The long axis of the trochlea is oriented transversely and slightly anterolaterally.

Morphology of the Hyobranchial Skeleton

The hyobranchial apparatus of *Gerrothorax* consists of several well ossified branchial arches that are ventrally grooved, indicative of fish-like internal gills. It was described by Nilsson (1946a), Hellrung (2003), Jenkins et al. (2008), and Schoch and Witzmann (2011), and therefore, the present description is restricted to hitherto neglected aspects of morphology and arrangement of the hyobranchial elements and to new observations. The rod-like basibranchial bone is slender, undifferentiated, and slightly broader anteriorly than posteriorly (Fig. 5C). Each ceratohyal bone has an elongate, oval shape and is the longest preserved element of the hyobranchium (Fig. 6). Approximately, the proximal half of the ventrolateral surface consists of a distinct depression with longitudinal striae at the proximal end. The distal end of the element bears similar longitudinal striae, but no depression is visible. Hypobranchial 1 is elongated rectangular in outline and bears a ventral ridge along the shaft that bifurcates at the distal broadening of the bone (Fig. 5C). Hypobranchials 2 and 3 are more slender and rod-like. Four pairs of ceratobranchials with dentigerous branchial platelets are present. Ceratobranchial 1 is almost straight, whereas the posteriorly following three elements get increasingly curved and shorter (Fig. 6). Each ceratobranchial is widened proximally in a triangular extension and tapers continuously in a distal direction. A broad, shallow ridge extends from the proximal end distally. It divides the ventral side of the proximal triangular expansion in two concave fields. The broad ridge increases distinctly in height at the transition from the triangular expansion to the shaft and tapers into a rather sharp ventral crest. Two grooves extend along the lateral face of the shaft, a posteroventral and an anteroventral one.

DISCUSSION

Reconstruction of the Hyobranchial Apparatus

A reconstruction of the hyobranchial skeleton of *Gerrothorax* based mainly on SMNS 83866, MGUH 28919, and NRM-PZ B.18 is given in Figure 6. In contrast to Hellrung (2003) and Jenkins et al. (2008), who reconstructed a pair of large hypohyals in *Gerrothorax*, these bones are interpreted here as the first pair of hypobranchials for the following reasons. First, the ceratobranchials and not the ceratohyals are located distal to these elements in SMNS 83866 and MGUH 28919, and second, comparison with tetrapodomorph fishes (Jarvik, 1954, 1963; Downs et al., 2008), *Acanthostega* (Coates and Clack, 1991) and temnospondyls like *Dvinosaurus* (Bystrow, 1938) shows the hypohyals to be rather small elements proximal to the ceratohyals. If this interpretation is correct, then *Gerrothorax* has three pairs of hypobranchials instead of two pairs.

Reconstruction of Cranial and Hyobranchial Muscles

There have been only few attempts made to reconstruct cranial and hyobranchial muscles in stem-tetrapods and basal tetrapods. A careful reconstruction of the adductor jaw muscles of the trematosaurid stereospondyls *Lyrocephalus* and *Aphaneramma* was provided by Säve-Söderbergh (1945) based on comparison with the myology and skull anatomy of extant anurans and caudates. Carroll and Holmes (1980) investigated in depth the adductor muscles of several caudates and anurans. They projected the different portions of the adductors of caudates onto the skull roof of the microsaur *Hapsidopareion*, and those of anurans on the skull roof of the temnospondyls *Dendrerpeton* and *Doleserpeton*. Tentative reconstructions of parts of the jaw muscles in other basal tetrapods were provided by Wilson (1941), Olson (1961) and Beaumont (1977).

Adductor Jaw Musculature

Luther (1914), Lubosch (1938), Säve-Söderbergh (1945), and Carroll and Holmes (1980) distinguished three portions of the adductor musculature

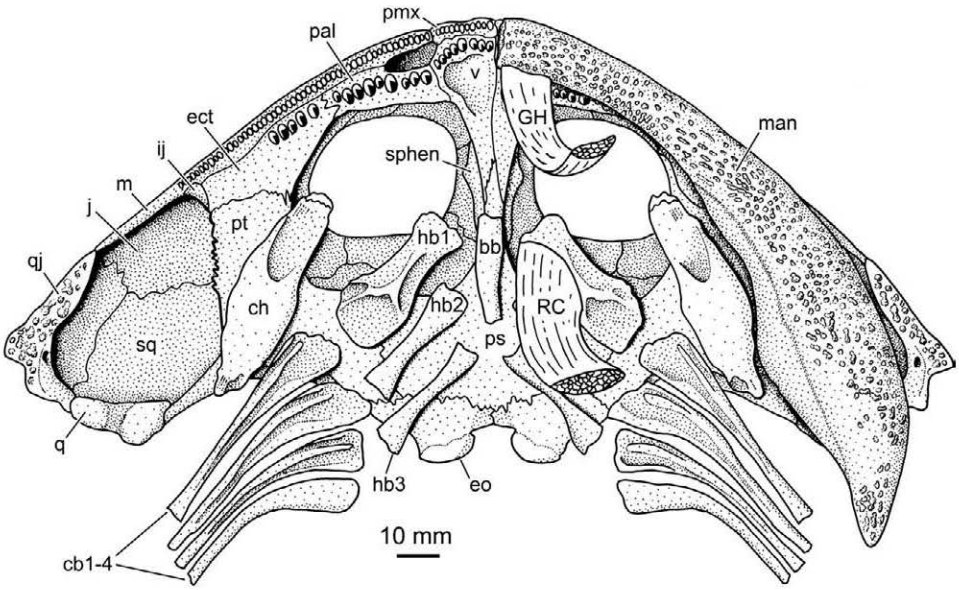

Fig. 6. Reconstruction of skull and hyobranchial apparatus of *Gerrothorax pulcherrimus* in ventral view. The mandible and two presumed muscles are shown on the left side. Based on SMNS 83866, 84787, 84791, 91354, MGUH 28919, and NRM-PZ B.18. bb, basibranchial; cb, ceratobranchial; ch, ceratohyal; ect, ectopterygoid; eo, exoccipital; GH, geniohyoideus; hb, hypobranchial; ij, insula jugalis; j, jugal; m, maxilla; man, mandible; pal, palatine; pmx, premaxilla; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; RC, rectus cervicis; sphen, sphenethmoid; sq, squamosal; v, vomer.

in extant anurans and caudates, based on their position relative to the three branches of the trigeminal nerve: the adductores mandibulae externus, posterior and internus. Carroll and Holmes (1980) divided the adductor mandibulae posterior into three further parts, the adductores mandibulae posterior longus, lateralis and articularis. In contrast to this nerve-based homologization of adductor musculature, Haas (2001) and Johnston (2011) found the course of the trigeminal nerve being variable and thus not necessarily the defining feature in homology of adductor muscles in lissamphibians and used the topology of origins, insertions, and fiber directions as defining characters (see also Iordanskij, 1990). Johnston (2011) recognized an adductor mandibulae posterior (adductor mandibulae posterior articularis of Carroll and Holmes, 1980, and levator mandibulae articularis of Haas, 2001) as a separate entity and termed the adductores mandibulae posterior longus and lateralis *sensu* Carroll and Holmes (1980) as adductores mandibulae longus and lateralis, respectively.

Although we principally adopt the terminology of Haas (2001) and Johnston (2011), we found only evidence for three adductor muscle portions in *Gerrothorax*: M.a. internus (=internus and longus of Haas, 2001), M.a. posterior, and M.a.externus.

The muscle attachment sites described above suggest a powerful adductor musculature. These muscles attached on the ventral side of the dermal skull roof (squamosal including descending lamina, quadratojugal, jugal, parietal and frontal), the pterygoid and quadrate, but also on the mandible (adductor chamber, preglenoid process). However, the following attempt to distinguish the particular portions of this muscle in *Gerrothorax* is admittedly difficult and remains somewhat hypothetical.

The adductor mandibulae externus most probably inserted on the lateral part of the squamosal bone, the posterior part of the jugal bone, and the medial part of the quadratojugal bone (Fig. 7A; direct evidence by scars, pits, and depressions). The extent of this muscle was limited laterally by the dermal bones of the cheek, anteriorly by the anterior margin of the subtemporal fenestra with the presumed tendon for the anterior muscle portion (see below), and medially by the adductores posterior and internus. The adductor mandibulae externus inserted within the adductor fossa. The muscle scars give no evidence of the fiber orientation in the living animal.

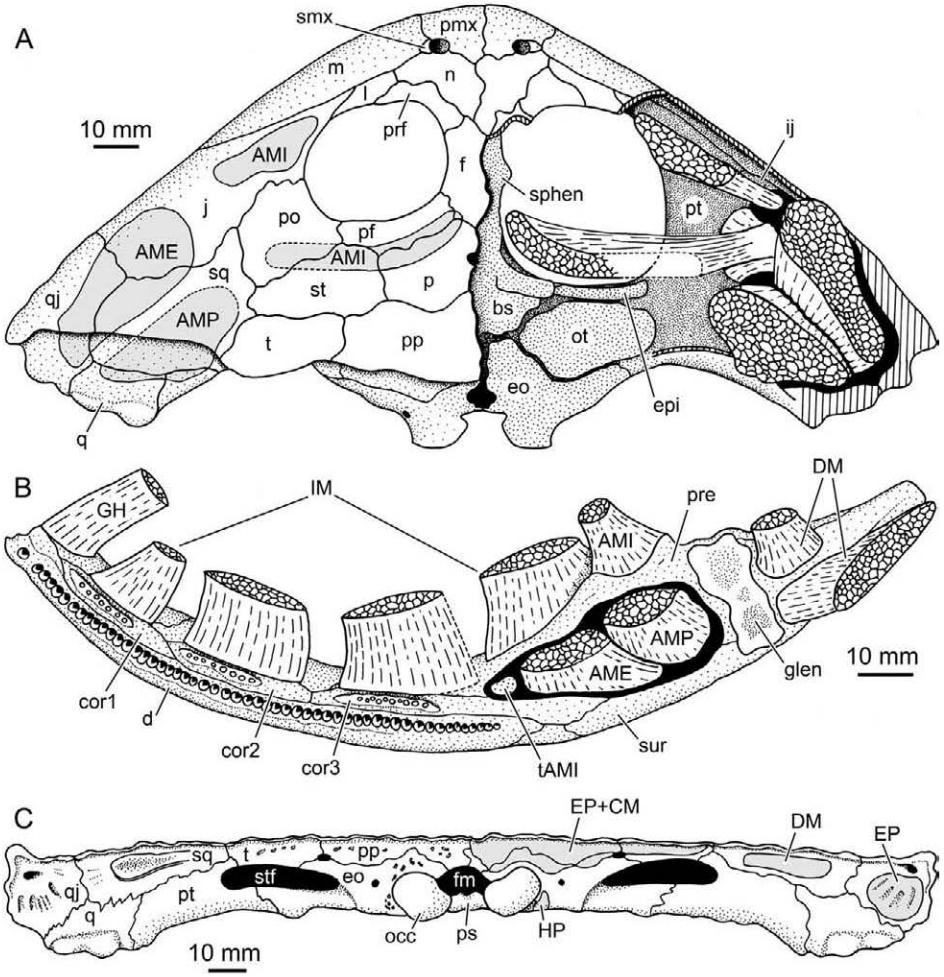

Fig. 7. Reconstruction of muscle attachment sites and muscles based on ossified muscle attachment sites in the skull of *Gerrothorax pulcherrimus*. (**A**) Reconstruction of skull in dorsal view. The presumed outline of jaw adductor attachment sites on the ventral side of the skull roof are shown in gray on the left side of the skull; most of the skull roofing bones are removed on the right side, exposing the endocranial bones and the presumed adductor muscles. Based mainly on SMNS 83866, 84786 and 84788. (**B**) Reconstruction of left mandibular ramus in dorsal view with presumed adductor, depressor, and hyobranchial muscles. From AME and AMP, no scars are preserved in the adductor fossa; they are reconstructed here on the basis of their scars on the dermal skull roof. (**C**) Reconstruction of skull in occipital view, based mainly on SMNS 84788. The presumed outline of epaxial, depressor, and cleidomastoideus muscle attachment sites is shown in gray on the right half of the skull. AME, adductor mandibulae externus; AMI, adductor mandibulae internus; AMP, adductor mandibulae posterior; bs, basisphenoid; CM, cleidomastoideus; cor, coronoid; d, dentary; DM, depressor mandibulae; eo, exoccipital; EP, epaxial muscles; epi, epipterygoid; f, frontal; fm, foramen magnum; GH, geniohyoideus; glen, glenoid; HP, hypaxial muscle; ij, insula jugalis; IM, intermandibularis; j, jugal; l, lacrimal; m, maxilla; n, nasal; occ, occipital condyle; ot, otic capsule; p, parietal; pf, postfrontal; pmx, premaxilla; po, postorbital; pp, postparietal; pre, prearticular; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; smx, septomaxilla; sphen, sphenethmoid; sq, squamosal; st, supratemporal; stf, subtympanic fossa; sur, surangular; t, tabular; tAMI, tendon for anterior portion of adductor mandibulae internus.

The anteroposteriorly aligned scars on the quadrate bone and the anteroposteriorly and anteromedially aligned scars on the posteromedial part of the squamosal bone probably represent the site of origin of the posterior adductor mandibulae muscle (Fig. 7A). This muscle was directed toward the adductor chamber of the mandible; there is no direct evidence of insertion at the Meckelian fenestra as reconstructed by Carrol and Holmes (1980) for *Dendrerpeton,* because this region is poorly preserved in the investigated material. The extent of this muscle was limited laterally by the external adductor mandibulae muscle, posteriorly by the lamina descendens of the squamosal bone, anteromedially probably by the internal adductor mandibulae muscle and medially by the quadrate ramus of pterygoid bone.

The m. adductor mandibulae internus originated probably from the parietal and frontal bones (evidence by anteroposteriorly oriented scars), possibly postfrontal and supratemporal bones (no direct evidence), the lateral and dorsolateral parts of the palatine ramus of the pterygoid bone (evidence by laterally oriented striae and projections) and probably the sphenethmoid and epipterygoid bones, which are well ossified in *Gerrothorax*, but poor preservation of the bone surface precludes recognition of muscle attachment sites. This muscle inserted probably at the lingual face of the adductor chamber of the mandible, especially the preglenoid process (direct evidence of muscle scars; Fig. 7A,B). The extent of this muscle was limited anteriorly by the orbital margin (more precisely the sculptured areas of the orbital rim), anteriorly and medially probably by the sphenethmoid and posteriorly by the epipterygoid and the otic capsule. A long preorbital portion of the internal adductor muscle can be assumed in *Gerrothorax*, which is indicated by the morphology of the insula jugalis (Fig. 7A). As described earlier, the insula jugalis has the appearance of a trochlea and might have served as a role for a tendon of a muscle that inserted in the center and the more anterior portion of the jugal, as indicated by numerous large pits in this region. Because of the flattening of the skull in this region, this muscle was probably aligned at a flat angle anterior to the insula jugalis and was located ventrolateral to the large orbits. Most probably, the tendon was directed into the anterior part of the adductor fossa of the mandible and probably attached to the boss on the floor of this fossa. A preorbital part (consisting of preorbitalis superficialis and profundus) of the internal adductor muscle is present in basal actinopterygians and extends ventral to the eye (Lauder, 1980), and according to Luther (1914), an anterior (= preorbital) part of the adductor internus muscle may reach below the eye anteriorly in certain caudates and gymnophionans. The preorbitalis of basal actinopterygians is probably homologous with the pseudotemporal part of the internal adductor muscle of anurans and caudates. A similar anterior extension of a part of the adductor musculature via a bony trochlea as supposed here in *Gerrothorax* was assumed by Beaumont (1977) in baphetids. However, in baphetids, the muscle was probably attached to an anterior extension of the orbit, whereas in *Gerrothorax*, this was not possible because the sculptured orbital rim indicates the coverage by dermis of this region (see above).

Depressor musculature. A depressor mandibulae is present in batrachians (i.e., anurans and caudates), which is double-headed in certain taxa and single-headed in others (Luther, 1914; Carroll and Holmes, 1980; Iordanskij, 1990; Bauer, 1997; Kleinteich and Haas, 2011). Thus, it cannot be decided at the moment if the presence of two distinct portions or of only one portion is plesiomorphic for batrachians. Uniquely among osteichthyan fishes, dipnoans possess also a depressor mandibulae, but its homology with that of tetrapods has been disputed (e.g., Edgeworth, 1935; Bemis, 1986; Bemis and Lauder, 1986). Also, Bauer (1997) pointed out that the "depressor mandibulae" in dipnoans is not homologous to the depressor mandibulae of tetrapods. Rather, it represents a specialized portion of the hyoid constrictor sheet sensu stricto, which is functionally and topographically comparable to the depressor of tetrapods. According to Diogo et al. (2008a), however, the m. depressor mandibulae of dipnoans is apparently homologous with part of the tetrapod depressor, that is, with the m. depressor mandibulae anterior of lissamphibians. As described earlier, the dorsal surface of the large postglenoid area consists of two different parts, a deep, anteroposteriorly elongate trough of the surangular and medial to it a faintly concave area with a large foramen on the articular. Both areas can be interpreted as attachment sites of the depressor musculature, so that the m. depressor mandibulae consisted at least of two portions in *Gerrothorax* (Fig. 7B). The orientation of the numerous muscle scars within the surangular trough indicates that this portion of the depressor was aligned dorsoposteriorly, probably toward a dorsal fascia posterior to the skull as site of origin. As suggested by Shishkin (1987), Jenkins et al. (2008), and Witzmann et al. (2012), the portion of the depressor that inserted on the articular bone was directed anteromedially, and probably originated on the ovate raised area on the occipital face of the squamosal bone.

Axial muscles. The axial musculature of the anterior trunk region, that is, epaxial and hypaxial (subvertebral) muscles, may move or stabilize the skull relative to the vertebral column and is thus important in tetrapod feeding. In extant caudates, muscle attachment sites may be found at the posterior end of the parietals for epaxial muscles, and the posterior part of the parasphenoid and

posterolateral parts of the skull might bear attachment points for the hypaxial muscles (Erdman and Cundall, 1984). In basal actinopterygians (Lauder, 1980) and the extant lungfish *Neoceratodus* (Bemis, 1986), the epaxial muscles insert on the posterodorsal margin of the skull. In *Gerrothorax*, distinct tuberosities posterior to the sculptured bone surface indicate the presence of strong epaxial muscles that were attached along the occipital lamellae of postparietals and tabulars (Fig. 7C). Further attachment sites of epaxial musculature are the tuberosities described earlier on the exoccipital bones. In addition, the occipital face of the quadratojugal bone forms a large, concave area with distinct muscle scars. Plagiosaurids are derived in possessing very small posttemporal fossae (Shiskin, 1987; Jenkins et al., 2008; Witzmann et al., 2012), which might even be absent in some individuals, either on one or on both sides of the skull. The posttemporal fossae of basal tetrapods, which are homologous with the fossa bridgei of sarcoptyergian fishes (Jarvik, 1954; Clack, 1998), are usually interpreted as area of origin of epaxial muscles (Olson, 1936; Romer and Witter, 1942). Similar to plagiosaurids, embolomeres have also lost the posttemporal fossae (Clack and Holmes, 1988), probably associated with the elaboration of tabular facets and elongate tabular horns, which provided further attachment sites of epaxial musculature (Clack, 1998). In plagiosaurids, the loss or reduction of the posttemporal fossae might be associated with the loss of the squamosal embayment (or otic notch), leading to a larger attachment surface for epaxial muscles on the occipital faces of tabular, squamosal and quadratojugal.

The distinct tubercles and rugosities on the lateral and ventrolateral surface of the condylar process of the exoccipital found by Witzmann et al. (2010) can best be interpreted as attachment sites of hypaxial muscles. Jenkins et al. (2008) found a distinct ventrolateral tubercle on the condylar process of the exoccipital but did not comment on this. Boy (1971) described similar tubercular structures on the condylar process of *cf. Glanochthon* and interpreted it as attachment site of axial musculature. This corresponds to the situation in extant caudates (Lubosch, 1938; Erdman and Cundall, 1984), in which superficial lateral fibers of the hypaxial (subvertebralis) muscle attach to the ventral surface of the exoccipitals and parasphenoid; in extant basal actinopterygians, a division of the hypaxialis muscle, the obliquus superioris, inserts on the posterolateral margin of the skull (Lauder, 1980).

Musculus cleidomastoideus. The mammalian m. cleidomastoideus is a branchiomeric neck muscle that connects bones of the shoulder girdle with the occipital and temporal region of the skull. Together with further neck muscles, it is homologous to the reptilian trapezius and sternocleidomastoideus muscle, and thus corresponds to the protractor pectoralis muscle of osteichthyan fishes and amphibians (Diogo et al., 2008b). The cleidomastoideus (or protractor pectoralis) is supposed to have linked the cleithrum and the region of the tabular in capitosaur stereospondyls (Howie, 1970; Sulej and Majer, 2005). The presence of this muscle was also suggested in plagiosaurids by Howie (1970), Shiskin (1987), and Jenkins et al. (2008). According to phylogenetic reasoning as well as the muscle attachment sites on the occipital face of the skull (see above) and the structure of the anteroposteriorly elongate cleithrum (Nilsson, 1946b; Jenkins et al., 2008), this is reasonable. However, a distinction between the attachment sites of cleidomastoideus and epaxial muscles on the occipital face of the skull cannot be undertaken.

Hyobranchial musculature. From the hyobranchial musculature, the intermandibularis, geniohyoideus, and rectus cervicis can be reconstructed with confidence. The reconstruction of ventral branchial muscles, in contrast, is more difficult and the assignment of particular muscles remains ambiguous.

The presence of intermandibular musculature, consisting of the intermandibularis anterior and posterior and the interhyoideus, is plesiomorphic for osteichthyans (Lauder, 1980). These muscles also occur in extant caudates (e.g., Drüner, 1901, 1904; Deban and Wake, 2000; Kleinteich and Haas, 2011) and can thus be assumed to be present in temnospondyls. There is direct evidence for large intermandibular muscle sheets in *Gerrothorax*, shown by the above described rugosities on the coronoids, the distinct ventromedial furrow on the mandible, and the medially concave surface of the splenials (Fig. 7B). However, a distinction between anterior and posterior intermandibular muscles in *Gerrothorax* would be arbitrary. The intermandibularis muscles act as hyobranchial stabilizers and levators (Deban and Wake, 2000).

The posterior attachment site of the mandibular symphysis is indicative of an anteroposteriorly aligned muscle, which is interpreted here as the geniohyoideus muscle (Figs. 6 and 7B). In extant caudates, this muscle originates at the symphyseal region and inserts on the basihyal (Deban and Wake, 2000; Kleinteich and Haas, 2011). In *Cryptobranchus*, the geniohyoideus inserts posteriorly on the ventral epimysium of the rectus cervicis muscle, and its deeper fibers terminate in a tendon attached to the second hypobranchial (Elwood and Cundall, 1994). The geniohyoideus of tetrapods corresponds to the branchiomandibularis muscle of basal actinopterygians (Lauder, 1980; Kanyukin, 2006), which originates near the mandibular symphysis and inserts posteriorly on the third hypobranchial. It is hypothesized here that deeper fibers of this muscle in *Gerrothorax* might have inserted on the anterior edge of the ventral

longitudinal crest of the broad, elaborate first pair of hypobranchials. The geniohyoideus acts as hyobranchial levator, but it is also used for lower jaw depression (Deban and Wake, 2000).

In basal actinopterygians, the rectus cervicis (or sternohyoideus) connects the hypohyals and the pectoral girdle and acts in mandibular and hyoid depression (Lauder, 1980). In many extant caudate larvae, the rectus cervicis muscle extends from the basibranchial and hypobranchial 1 to the pectoral girdle (Jarvik, 1963; Erdman and Cundall, 1984) and exerts caudal force on the center of the hyobranchial apparatus, thus acting as a hyobranchial depressor (Deban and Wake, 2000). In *Gerrothorax*, this muscle was apparently strongly developed; the posteromedial edge of the ventral longitudinal crest of the well ossified hypobranchial 1 can be interpreted as its insertion side (Fig. 6). The prominent hypobranchial 1 probably compensated for the rather small, slender basibranchial that was incompletely ossified and which shows no muscle scars or attachment sites. The m. rectus cervicis was attached posteriorly to the anterodorsal surface of the large interclavicle.

In extant fish-like sarcopterygians (dipnoans and *Latimeria*), the interarcualis ventralis 1 muscle connects the hyoid arch and the proximal part of ceratobranchial 1, and interarcualis ventralis 2–5 connect the proximal parts of the ceratobranchials with each other (Wiley, 1979). Interarcualis ventralis muscles are absent in actinopterygians. The ventral branchial muscles in larvae of caudates and gymnophionans consist of subarcualis rectus 1 that originates on the ceratohyal bone and inserts on ceratobranchial 1, subarcualis recti 2–4, that connect ceratobranchial 4 with ceratobranchial 1 and have additional insertion sites on ceratobranchials 2 and 3, respectively, and subarcualis obliquus 2 and 3, that connect ceratobranchials 2 and 1 as well as ceratobranchials 3 and 2, respectively (Jarvik, 1963; Deban and Wake, 2000; Kleinteich and Haas, 2007, 2011). The subarcualis rectus and obliquus muscles adduct the ceratobranchials medially in larval caudates and may open or close the gill slits (Deban and Wake, 2000). Homology of interarcualis ventralis muscles in fishlike sarcopterygians and the subarcualis rectus and obliquus muscles in larval caudates is not yet established. However, the depressed area and striae on the anterior part of the ventral surface of the ceratohyal in *Gerrothorax* (Fig. 6) might suggest the origination of a muscle comparable to interarcualis ventralis 1 or subarcualis rectus 1. Furthermore, the distinct ventral crest on the expanded proximal ends of the ceratobranchials strongly suggests the insertion sites of a well developed ventral branchial musculature. Therefore, a powerful ventral branchial musculature can be reconstructed in *Gerrothorax*, although the designation of the muscles remains uncertain.

Feeding in Plagiosaurids: History of Subject

The question how the aberrant morphology of plagiosaurids relates to feeding has puzzled paleontologists for decades. Panchen (1959), elaborating a on a hypothesis suggested by Watson (1919, 1951, 1958) for capitosaur stereospondyls, suggested that plagiosaurids lived at the water bottom and that they opened the mouth by cranial elevation rather than mandible abduction. According to this hypothesis, raising the skulls was accomplished by epaxial and depressor mandibulae muscles while the mandibles rested on the substrate. Howie (1970), in contrast, ruled out the head-lifting function of the depressor mandibulae in flat-headed temnospondyls. She suggested the cleidomastoideus muscle as responsible for this function. Shishkin (1987) agreed with the proposed role of the cleidomastoideus muscle in plagiosaurids but concomitantly emphasized the importance of the epaxial musculature in raising the skull. Panchen (1959), Howie (1970) and Shishkin (1987) assumed a rather horizontal position of the skull of plagiosaurids before it was raised for prey capture. In contrast, Hellrung (2003) suggested that the skull of *Gerrothorax* was held at an elevated posture of ca. 30° with the mouth closed, producing sufficient interspace between palate and interclavicle and thus enabling depression of the buccal floor during prey capture. In a detailed study of the neck joint in *Gerrothorax*, Jenkins et al. (2008) were recently able to show that raising of the skull occurred by atlanto-occipital rotation that slightly protruded the mandible, which in turn was hardly depressed. In all these proposed jaw opening mechanisms, the function of the hyobranchial apparatus was not considered. Among extant caudates, larval morphs and neotenic taxa have a hyobranchial apparatus that closely resembles that of *Gerrothorax*. In these extant taxa, the similarly arranged hyobranchial elements play a major role in mouth opening and prey capture by depressing and raising the buccal floor and generate powerful suction for suction feeding (e.g., Deban and Wake, 2000). In the scenarios provided by Panchen (1959), Howie (1970), Shishkin (1987), and Jenkins et al. (2008), the hyobranchial apparatus remained rather stationary during mouth opening, and as the mandibles rested on the ground, no ventral movement of the buccal floor was possible. However, the robust nature of the almost completely ossified hyobranchial apparatus in *Gerrothorax* (and of other plagiosaurids; Schoch and Witzmann, 2011) strongly suggests an active role during prey capture.

Suction Feeding in Extant Aquatic Vertebrates

Extant osteichthyan fishes and caudate larvae capture prey items by using suction feeding (Matthes, 1934; Lauder, 1980; Lauder and Shaffer,

1985; Lauder and Reilly, 1994; Deban and Wake, 2000; Deban, 2003; Kleinteich and Haas, 2011). After initial mouth opening, the hyobranchium is rotated posteroventrally in osteichthyan fishes by action of the rectus cervicis muscle (sternohyoideus) and thus moves the floor of the mouth ventrally. The rectus cervicis (together with the levator operculi) also lowers the mandible, and epaxial muscles elevate the skull during this action. Maximum gape is reached before maximum posteroventral retraction of the hyobranchium, and after this, lateral opercular expansion occurs. The expansion of the mouth cavity causes negative pressure that generates a rapid flow of water and prey into the mouth. After beginning of mouth closure by action of the jaw adductors, the hyobranchial apparatus is protracted to its resting position by action of the geniohyoideus muscle and compresses the buccal cavity, expelling the water posterolaterally through the gill clefts. This kinematic pattern enables a unidirecional flow of water through the buccal cavity. In salamander larvae, the general pattern of suction feeding closely resembles that of osteichthyan fishes. The head is elevated by the epaxial muscles and the lower jaw is depressed by retraction of the hyobranchial apparatus, with the difference that the depressor mandibulae aids in jaw depression in larval salamanders. As in fishes, maximum gape is reached first and followed by maximum hyobranchial depression in larval salamanders. Both teleosts and larval salamanders have a kinetic skull, that is, cheek and maxilla can be rotated to control the amount and direction of water entering the buccal cavity and thus enhance the effectiveness of suction feeding. This is further supported by the presence of labial lobes along the lateral edges of the mouth in many aquatic salamanders, leading to a small, anterior mouth opening that enables directed suction.

Evidence in Cranial and Hyobranchial Morphology for Suction Feeding in *Gerrothorax*

Jenkins et al. (2008) demonstrated that *Gerrothorax* was able to elevate its skull through an angle of about 50°, suggesting that this large gape was achieved mainly by raising the skull. This action rotated the quadrate forward and slightly protruded the lower jaw, which was hardly lowered. Thus, *Gerrothorax* was able to capture prey while it rested on the floor of a water body. The study of Jenkins et al. (2008) is an important contribution to the feeding mechanism in *Gerrothorax* and other temnospondyls based especially on the investigation of the atlanto-occipital joint, but it shows only one aspect (mouth opening by skull elevation) and neglected the role of the hyobranchial apparatus during feeding. As this apparatus is extensively ossified in this plagiosaurid and bears prominent muscle attachment sites, it must be assumed that it was involved in capture of prey under water, more specifically, in expansion of the buccal cavity and thus in suction feeding.

The following aspects of skull and hyobranchial morphology indicate that *Gerrothorax* was able to prey by suction feeding in water. This temnospondyl has a broad, short-faced skull, which is a prerequisite for suction feeding (Taylor, 1987). The mouth opening is broad and directed anteriorly and only slightly laterally, so that the flow of water into the buccal cavity was directed and labial lobes were not necessary. The hyobranchial apparatus is robust and well ossified. According to Deban and Wake (2000), generating strong suction requires a well ossified, rigid hyobranchial apparatus, and strong associated hyobranchial muscles. At least a strong rectus cervicis can be reconstructed in *Gerrothorax* that was able to draw the hyobranchium rapidly in a posteroventral direction. Furthermore, the marginal teeth are rather slender and *Gerrothorax* does not possess large palatal or dentary fangs, so it can be assumed that it usually preyed on small- or middle-sized fishes or tetrapods that were not too large to be ingested by suction. The internal gills (Hellrung, 2003; Schoch and Witzmann, 2011) and branchial denticles on the ceratobranchials (Nilsson, 1946a; personal observations) indicate the presence of open gill clefts and thus unidirectional flow of water through the buccal cavity.

To our knowledge, however, not all aquatic temnospondyls relied on suction feeding. Skull shape and construction suggest that many edopoids, eryopids, and stereospondylomorphs were "crocodilomorph" feeding analogs (Damiani, 2001; Fortuny et al., 2011), that is, they used probably rapid sidewards sweeps of the head and direct biting, whereas the hyobranchial skeleton played a minor role.

Reconstruction of the Feeding Strike of *Gerrothorax*

The following is an attempt to reconstruct the feeding strike of *Gerrothorax* as far as can be inferred from skeletal anatomy and supposed associated soft parts (Fig. 8). It should be kept in mind, however, that numerous behavioral aspects during feeding cannot be deduced from the skeletal structure alone (e.g., Elwood and Cundall, 1994). The flattened morphology, the short limbs and tail and the heavily built skeleton strongly suggest that *Gerrothorax* was a bottom-dwelling ambush predator in freshwater and brackish environments like river channels, lakes, estuaries, and brackish swamps (Nilsson, 1946a; Hellrung, 2003; Jenkins et al., 2008; Schoch and Witzmann, 2012). However, if *Gerrothorax* rested on the bottom during prey capture and solely raised the head as

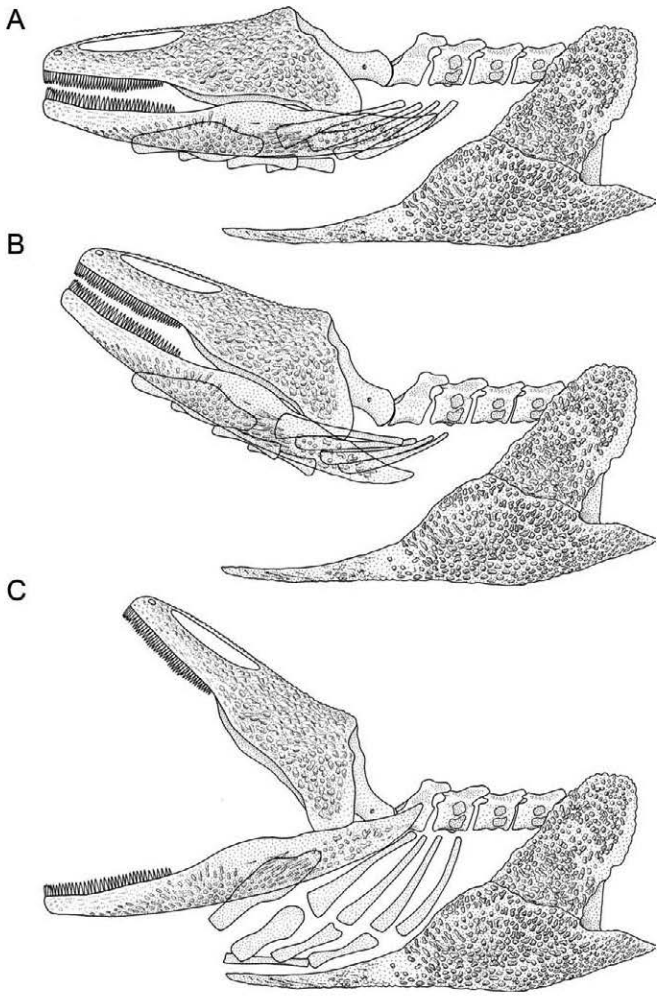

Fig. 8. Presumed movements of skull and hyobranchial skeleton of *Gerrothorax pulcherrimus* in lateral view during prey capture. (**A**) Skull is held horizontally with protracted hyobranchial apparatus (resting position). (**B**) Skull is lifted, the mouth is still closed, and the hyobranchial apparatus still protracted. (**C**) Mandible is lowered and the hyobranchial apparatus is drawn ventrally and caudally to expand the buccal cavity. Skull and pectoral girdle based on specimen SMNS 83070, vertebrae drawn after Jenkins et al. (2008).

suggested by Jenkins et al. (2008), there would have been by far not enough interspace between skull and pectoral girdle to retract the hyobranchial apparatus and to increase the size of the buccal cavity for suction feeding. Furthermore, the muscle scars on the postglenoid area indicate that a portion of the depressor mandibulae extended backwards on the back of the trunk behind the skull. This suggests that the depressor was indeed used for lowering the mandible and not to raise the skull as earlier supposed (Panchen, 1959) and implies that the skull including the mandible must have been lifted off the ground during prey capture. It can thus be assumed that when bypassing prey was recognized by *Gerrothorax* (by the lateral line system, olfaction and/or vision) it raised the head (and possibly also the anterior trunk region) toward the prey with the jaws still closed. Then

the mouth started to open rapidly. This was caused by (1) raising the head as shown by the extant bracketing taxa basal osteichthyans (Lauder, 1980), extant dipnoans (Bemis, 1986) and aquatic caudates (Lauder and Shaffer, 1985), by action of strong epaxial muscles and probably the cleidomastoideus muscle (Howie, 1970; Jenkins et al., 2008), and (2) by lowering the mandible by action of the strong depressor mandibulae and the rectus cervicis muscle. During further elevation of the skull, the action of the rectus cervicis rotated the hyobranchial apparatus ventrally and caudally, thus expanding the buccal cavity and causing the inflow of water plus prey through the mouth opening. The obviously strong depressor mandibulae, the well ossified, large quadrate-articular joint and the powerful rectus cervicis suggest that this action occurred rapidly and that strong suction was generated. As bracketing by extant basal osteichthyans and caudate larvae (Lauder, 1980; Lauder and Shaffer, 1985; Lauder and Reilly, 1994) suggests, maximum hyobranchial retraction occurred after maximum gape. The m. geniohyoideus pulled the hyobranchium anterodorsally, and water was expelled through the opened gill clefts. The captured prey item was seized by pressure of the hyobranchial apparatus against the palate (the parasphenoid is toothed in at least some individuals of *Gerrothorax*; Schoch and Witzmann, 2012) and was probably moved toward the esophagus by a posteriorly directed current of water as in larvae of caudates as well as in actinopterygians and dipnoans (Lauder and Reilly, 1994). The dentigerous branchial platelets situated on the ceratobranchials prevented the prey from escaping through the gill clefts (Witzmann, 2004). Similar to the jaw opening muscles, also the jaw adductors were well developed as indicated by the above described osteological correlates, enabling also a rapid closure of the mouth.

Despite the similarities of the feeding mechanism in *Gerrothorax* to that in extant caudate larvae, a striking difference exist: unlike in extant caudate larvae and many derived actinopterygians (teleosts), no cranial kinesis was possible in the *Gerrothorax* skull, because all sutures of skull roof and palate are rigid and no moveable articulation of skull bones was present, neither in the skull roof nor in the palate. An akinetic skull roof is characteristic for the vast majority of temnospondyls and is probably plesiomorphic for tetrapods in general; in this respect, the skull of *Gerrothorax* and most temnospondyls resemble those of basal actinopterygians (Lauder, 1980; Janvier, 1996).

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LITERATURE CITED

Allis EP. 1897. The cranial muscles and cranial and first spinal nerves in *Amia calva*. J Morphol 12:487–772.

Allis EP. 1922. The cranial anatomy of *Polypterus*, with special reference to *Polypterus bichir*. J Anat 56:189–291.

Bauer WJ. 1997. A contribution to the morphology of visceral jaw-opening muscles of urodeles (Amphibia: Caudata). J Morphol 233:77–97.

Beaumont E. 1977. Cranial morphology of the Loxommatidae (Amphibia: Labyrinthodontia). Philos Trans R Soc Lond B Biol Sci 280:29–101.

Bemis WE. 1986. Feeding systems of living Dipnoi: Anatomy and function. J Morphol 190 Suppl 1:249–275.

Bemis WE, Lauder GV. 1986. Morphology and function of the feeding apparatus of the lungfish, *Lepidosiren paradoxa* (Dipnoi). J Morphol 187:81–108.

Boy JA. 1971. Ein bemerkenswerter Schädelrest eines unterpermischen Labyrinthodontiers (Amphibia) aus dem Saargebiet. Abh hess L-Amt Bodenforsch 60:31–43.

Bystrow AP. 1938. *Dvinosaurus* als neotenische Form der Stegocephalen. Acta Zool (Stockholm) 19:209–295.

Carroll RL, Holmes R. 1980. The skull and jaw musculature as guides to the ancestry of salamanders. Zool J Linn Soc 68: 1–40.

Castanet J, Francillon-Vieillot H, Ricqlès A de, Zylberberg L. 2003. The skeletal histology of the Amphibia. In: Heatwole H, Davies M, editors. Amphibian Biology: Osteology, Vol. 5. Chipping Norton: Surrey Beatty. pp 1598–1683.

Clack JA. 1998. The neurocranium of *Acanthostega gunnari* Jarvik and the evolution of the otic region in tetrapods. Zool J Linn Soc 122:61–97.

Clack JA, Holmes RR. 1988. The braincase of the anthracosaur *Archeria crassidisca* with comments on the interrelationships of primitive tetrapods. Palaeontology 31:85–107.

Cloutier R, Ahlberg PE. 1996. Morphology, characters, and the interrelationships of basal sarcopterygians. In: Stiassny MLJ, Parenti LR, Johnson GD, editors. Interrelationships of Fishes. San Diego, CA: Academic Press. pp 445–480.

Coates MI, Clack JA. 1991. Fish–like gills and breathing in the earliest known tetrapod. Nature 352:234–236.

Damiani RJ. 2001. Cranial anatomy of the giant Middle Triassic temnospondyl *Chernia megarhina* and a review of feeding in mastodonsaurids. Palaeont Afr 37:41–52.

Damiani RJ, Schoch RR, Hellrung H, Werneburg R, Gastou S. 2009. The plagiosaurid temnospondyl *Plagiosuchus pustulifer*us from the Middle Triassic of Germany: Anatomy and functional morphology of the skull. Zool J Linn Soc 155:348–373.

Deban SM. 2003. Constraint and convergence in the evolution of salamander feeding. In: Bels VL, Gasc J-P, Casinos A, editors. Vertebrate Biomechanics and Evolution. Oxford: BIOS Scientific Publishers Ltd. pp 161–178.

Deban SM, Wake DB. 2000. Aquatic feeding in Salamanders. In: Schwenk K, editor. Feeding: Form, Function and Evolution in Tetrapod Vertebrates. San Diego: Academic Press. pp 65–94.

Dias-da-Silva S, Milner AR. 2010. The pustulated temnospondyl revisited—A plagiosternine plagiosaurid from the Lower Triassic of Brazil. Acta Palaeontol Pol 55:561–563.

Diogo R, Hinits Y, Hughes S. 2008a. Development of mandibular, hyoid and hypobranchial muscles in the zebrafish: Homologies and evolution of these muscles in bony fishes and tetrapods. BMC Dev Biol 8:24–46.

Diogo R, Abdala V, Lonergan N, Wood BA. 2008b. From fish to modern humans—Comparative anatomy, homologies and evolution of the head and neck musculature. J Anat 213: 391–424.

Downs JP, Daeschler EB, Jenkins FA, Shubin NH. 2008. The cranial endoskeleton of *Tiktaalik roseae*. Nature 455:925–929.

Drüner L. 1901. Studien zur Anatomie der Zungenbein-, Kiemenbogen- und Kehlkopfmuskulatur der Urodelen. I. Theil. Zool Jahrb Anat Ontog 15:435–622.

Drüner L. 1904. Studien zur Anatomie der Zungenbein-, Kiemenbogen-, und Kehlkopmuskeln der Urodelen. II. Theil. Zool Jahrb Anat Ontog 19:361–690.

Edgeworth FH. 1935. The Cranial Muscles of Vertebrates. Cambridge: Cambridge University Press.493 p.

Elwood JRL, Cundall D. 1994. Morphology and behavior of the feeding apparatus in *Cryptobranchus alleganiensis* (Amphibia: Caudata). J Morphol 220:47–70.

Erdman S, Cundall D. 1984. The feeding apparatus of the salamander *Amphiuma tridactylum*: Morphology and behavior. J Morphol 181:175–204.

Fortuny J, Marcé-Nogué J, de Esteban-Trivigno S, Gil L, Galobart À. 2011. Temnospondyli bite club: Ecomorphological patterns of the most diverse group of early tetrapods. J Evol Biol 24:2040–2054.

Fox H. 1954. Development of the skull and associated structures in the Amphibia with special reference to the urodeles. Trans Zool Soc Lond 28:241–302.

Fraas E. 1913. Neue Labyrinthodonten aus der schwäbischen Trias. Palaeontographica 60:275–294.

Haas A. 2001. Mandibular arch musculature of anuran tadpoles, with comments on homologies of amphibian jaw muscles. J Morphol 247:1–33.

Hellrung H. 2003. *Gerrothorax pustuloglomeratus*, ein Temnospondyle (Amphibia) mit knöcherner Branchialkammer aus dem Unteren Keuper von Kupferzell (Süddeutschland). Stuttg Beitr Natkd Ser B 330:1–130.

Hennig W. 1966. Phylogenetic Systematics. Champaign, IL: University of Illinois Press.280 p.

Howie AA. 1970. A new capitosaurid labyrinthodont from East Africa. Palaeontology 13:210–253.

Iordanskij NN. 1990. Evolution of Complex Adaptations: The Jaw Apparatus of Amphibians and Reptiles. Moscow: Nauka.310 p.

Janvier P. 1996. Early Vertebrates. Oxford: Clarendon Press. 393 p.

Jarvik E. 1954. On the visceral skeleton in *Eusthenopteron* with a discussion of the parasphenoid and palatoquadrate in fishes. K Svenska Vet Akad Handl, Ser. 4, 5,1:1–104.

Jarvik E. 1963. The composition of the intermandibular division of the head in fish and tetrapods and the diphyletic origin of the tetrapod tongue. K Svenska Vet Akad Handl, Ser. 4, 9,1:1–74.

Jenkins FA Jr, Shubin NH, Gatesy SM, Warren AA. 2008. *Gerrothorax pulcherrimus* from the Upper triassic Fleming Fjord formation of East Greenland and a reassessment of head lifting in temnospondyl feeding. J Vertebr Paleontol 28:935–950.

Johnston P. 2011. Cranial muscles of the anurans *Leiopelma hochstetteri* and *Ascaphus truei* and the homologies of the mandibular adductors in Lissamphibia and other gnathostomes. J Morphol 272:1492–1512.

Kanyukin AA. 2006. Hyobranchial skeleton and hypobranchial muscles of rhipidistians. Paleontol J 40:297–311.

Kleinteich T, Haas A. 2007. Cranial musculature in the larva of the caecilian, *Ichthyophis kohtaoensis* (Lissamphibia: Gymnophiona). J Morphol 268:74–88.

Kleinteich T, Haas A. 2011. The hyal and ventral branchial muscles in caecilian and salamander larvae: Homologies and evolution. J Morphol 272:598–613.

Lauder GV. 1980. Evolution of the feeding mechanism in primitive actinopterygian fishes: A functional anatomical analysis of *Polypterus, Lepisosteus* and *Amia*. J Morphol 163:283–317.

Lauder GV, Reilly SM. 1994. Amphibian feeding behavior: Comparative biomechanics and evolution. In: Bels M, Chardon P, Vandewalle P, editors. Biomechanics of Feeding in Vertebrates. Advances in Comparative and Environmental Physiology, Vol. 18. Berlin: Springer Verlag. pp 163–195.

Lauder GV, Shaffer BH. 1985. Functional morphology of the feeding mechanism in Aquatic Ambystomatid Salamanders. J Morphol 185:297–326.

Lubosch W. 1938. Muskeln des Kopfes: Viscerale Muskulatur. In: Bolk L, Göppert E, Kallius E, Lubosch W, editors. Handbuch der Vergleichenden Anatomie der Wirbeltiere. Band 5. Berlin: Urban und Schwarzenberg. pp.1011–1106.

Luther A. 1914. Über die vom N. trigeminus versorgte Muskulatur der Amphibien mit einem vergleichenden Ausblick über den Adductor mandibulae der Gnathostomen, und einem Beitrag zum Verständnis der Organisation der Anurenlarven. Acta Soc Scient Fenn 44:1–151.

Marjanović D, Laurin M. 2008. A reevaluation of the evidence supporting an unorthodox hypothesis on the origin of extant amphibians. Contrib Zool 77:149–199.

Matthes E. 1934. Bau und Funktion der Lippensäume wasserlebender Urodelen. Z Morphol Ökol Tiere 28:155–169.

Nilsson T. 1946a. A new find of *Gerrothorax rhaeticus* Nilsson, a plagiosaurid from the Rhaetic of Scania. Lunds Univ Arssk 42:1–42.

Nilsson T. 1946b. Structure of the cleithrum in plagiosaurids and the descent of Chelonia. Ark Zool 37:1–18.

Olson EC. 1936. The dorsal axial musculature of certain primitive Permian tetrapods. J Morphol 59:265–311.

Olson EC. 1961. Jaw mechanisms: Rhipidistians, amphibians, reptiles. Am Zool 1:205–215.

Panchen A. 1959. A new armoured amphibian from the Upper Permian of East Africa. Philos Trans R Soc Lond B Biol Sci 242:207–281.

Romer AS, Witter RV. 1942. Edops, a primitive rhachitomous amphibian from the Texas red beds. J Geol 50:925–960.

Ruta M, Coates MI. 2007. Dates, nodes and character conflict: Addressing the lissamphibian origin problem. J Syst Palaeontol 5:69–122.

Säve-Söderbergh G. 1945. Notes on the trigeminal musculature in non-mammalian tetrapods. Nov Act Regiae Soc Sci Upsaliensis Ser. 413:1–59.

Schoch RR. 2008. A new stereospondyl from the Middle Triassic of Germany, and the origin of the Metoposauridae. Zool J Linn Soc 152:79–113.

Schoch RR. The evolution of major temnospondyl clades—An inclusive phylogenetic analysis. J Syst Palaeontol (in press).

Schoch RR, Witzmann F. 2011. Bystrow's Paradox: Gills, fossils, and the fish-to-tetrapod transition. Acta Zool (Stockholm) 92:251–265.

Schoch RR, Witzmann F. 2012. Cranial morphology of the plagiosaurid *Gerrothorax pulcherrimus* as an extreme example of evolutionary stasis. Lethaia 45:371–385.

Shishkin MA. 1987. The evolution of early amphibians (Plagiosauroidea). Trudy Pal Inst Akad Nauk SSSR 225:1–143.

Sulej T, Majer D. 2005. The temnospondyl amphibian *Cyclotosaurus* from the Upper Triassic of Poland. Palaeontology 48:157–170.

Taylor MA. 1987. How tetrapods feed in water: A functional analysis by paradigm. Zool J Linn Soc 91:171–195.

Warren AA. 2000. Secondarily aquatic temnospondyls of the Upper Permian and Mesozoic. In: Heatwole H, Carroll RL, editors. Amphibian Biology: Palaeontology, Vol. 4. Chipping Norton: Surrey Beatty. pp 1121–1149.

Watson DMS. 1919. The structure, evolution and origin of the Amphibia. The "orders" Rhachitomi and Stereospondyli. Philos Trans R Soc Lond B Biol Sci 209:1–73.

Watson DMS. 1951. Paleontology and Modern Biology. New Haven, Connecticut: Yale University Press.216 p.

Watson DMS. 1958. A new labyrinthodont (*Paracyclotosaurus*) from the Upper Trias of New South Wales. Bull Br Mus Nat Hist 3:235–263.

Wiley EO. 1979. Ventral gill arch muscles and the interrelationships of gnathostomes, with a new classification of the Vertebrata. Zool J Linn Soc 67:149–179.

Wilson JA. 1941. An interpretation of the skull of *Buettneria*, with special reference to the cartilages and soft parts. Contrib Mus Paleontol Univ Mich 5:71–111.

Witmer LM. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In: Thomason J, editor. Functional Morphology in Vertebrate Paleontology. Cambridge: Cambridge University Press. pp 19–33.

Witzmann F. 2004. The external gills of Palaeozoic amphibians. N Jb Geol Pal Abh 232:375–401.

Witzmann F. 2011. Morphological and histological changes of dermal scales during the fish-to-tetrapod transition. Acta Zool (Stockholm) 92:281–302.

Witzmann F, Soler-Gijón R. 2010. The bone histology of osteoderms in temnospondyl amphibians and in the chroniosuchian *Bystrowiella*. Acta Zool (Stockholm) 91:96–114.

Witzmann F, Scholz H, Müller J, Kardjilov N. 2010. Sculpture and vascularization of dermal bones, and the implications for the physiology of basal tetrapods. Zool J Linn Soc 160: 302–340.

Witzmann F, Schoch RR, Hilger A, Kardjilov N. 2012. Braincase, palatoquadrate and ear region of the plagiosaurid *Gerrothorax pulcherrimus* (Fraas, 1913) from the Middle Triassic of Germany. Palaeontology 55:31–50.

Yates AM, Warren AA. 2000. The phylogeny of the "higher" temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. Zool J Linn Soc 128:77–121.

Zhu M, Schultze H-P. 2001. Interrelationship of basal osteichthyans. In: Ahlberg P, editor. Major Events in Early Vertebrate Evolution. London: Taylor and Francis. pp 289–314.

The hyobranchial apparatus in early tetrapods and its significance for feeding and breathing

Appendix 13

Witzmann, F. & Schoch, R. R. 2006. Skeletal development of the temnospondyl *Acanthostomatops vorax* from the Lower Permian Döhlen basin of Saxony. – Transactions of the Royal Society of Edinburgh: Earth Sciences 96: 365–385.

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Skeletal development of the temnospondyl *Acanthostomatops vorax* from the Lower Permian Döhlen Basin of Saxony

Florian Witzmann and Rainer R. Schoch

ABSTRACT: The development of the skeleton of the small temnospondyl *Acanthostomatops vorax* is described, based on 32 specimens from the Lower Rotliegend of Niederhäslich in Saxony. Both individually and ontogenetically, the skull table, length of gape, and dentition of the parasphenoid are broadly variable. The stapes has a short and straight shaft and a well-defined two-headed proximal region. Small specimens have three or four pairs of ossified ceratobranchials in the gill region, while the adult hyobranchium is composed of four pairs of hypobranchials and probably some additional elements. The postcranium is characterised by a stout and well-ossified humerus that is already large in small larvae, a minute rectangular interclavicle, a robust but short femur, a relatively short trunk with 21–22 presacrals and a moderate tail with 28 vertebrae. In adults, the trunk skeleton became proportionally shorter and the femur smaller with respect to skull length. Metamorphosis is best indicated by the disappearance of the larval gill skeleton, which was probably resorbed, while the structure of the limbs and axial skeleton as well as the absence of lateral line sulci suggest a terrestrial existence for adults.

KEY WORDS: Hyobranchium, metamorphosis, ontogeny, postcranium, Rotliegend, skull, variability, Zatracheidae.

The zatracheids form a small and still enigmatic clade of possibly terrestrial temnospondyls, which are well-defined by flat and wide, spine-bearing skulls, but whose postcrania are largely unknown. They fall within a larger group of temnospondyls with obvious terrestrial features, such as short bodies, strong limbs, and well-ossified girdles. This group includes the eryopids, dissorophoids and zatracheids, and since it was found monophyletic by Yates & Warren (2000) it has been referred to as the Euskelia. There are two major unsettled questions regarding this assemblage: (1) its potential status as a monophylum and (2) its relationship to the modern amphibians or Lissamphibia, as hypothesised by some authors (see Schoch & Milner 2004 for a recent overview). Both problems need much further work on poorly known members and a description of inadequately understood anatomical regions, with the zatracheids forming a small yet significant cornerstone in this field.

Zatracheids are known from only a few localities on two continents (North America and Europe), with two assemblages having yielded the bulk of the material: the Lower Permian Abo Formation in northern New Mexico, which has produced almost exclusively cranial material of *Zatrachys serratus*, and the Permo-Carboniferous Niederhäslich Formation of Dresden in Germany, which gave the partially articulated skeletons of *Acanthostomatops vorax*. After the initial descriptions provided by Geinitz & Deichmüller (1882), Credner (1883) and Case (1911), Langston (1953), Boy (1989) and Schoch (1997) have revised some aspects of this material, focusing mostly or exclusively on the skull. On the basis of these studies, recent analyses have concluded that zatracheids form a clade somehow related to dissorophoids (Holmes *et al.* 1998), eryopids (Boy 1990), or both (Schoch 1997; Yates & Warren 2000).

Despite the previous descriptions of *Acanthostomatops*, there remain numerous uncertainties regarding the postcranial skeleton, as well as the ontogeny of the entire skeleton. This study seeks to address these problems by reexamining Geinitz & Deichmüller's (1882) and Credner's (1883) original material, which since the end of the Cold War has become more freely accessible.

1. Material

All of the material comes from a thin layer of hard limestone from the same mine at Niederhäslich. It probably formed under lacustrine conditions (Schneider 1994). The skeletons are usually preserved as well-defined imprints, as the rather soft bone weathered easily to leave only a natural mould. In most cases, silicon casting of these moulds gives good results. The data presented here are based on examination of both silicon casts and original moulds.

Throughout the present paper, skull length is used as a measure of size, herein defined as the distance from the tip of the snout to the posterior margin of the postparietals. A total of 31 specimens of *Acanthostomatops* were investigated for this study, with individuals ranging from 13·5 mm to 75 mm in skull length (Fig. 1A). These specimens are housed in the following four institutions:

1. Landesamt für Umwelt und Geologie, Freiberg, Germany. When last described by Boy (1989), these specimens were still located in Dresden. (This material had different numbers before the 1990s, labelled 'S'). In the present study, we refer throughout to the new numbering. (LFUG): 13070 (ventral, 22 mm), 13214 (lectotype, ventral, 33 mm; Credner 1883, pl. 11, fig. 2), 13215 (ventral, 25 mm; Boy 1989, fig. 2a), 13221 (dorsal, circa 17 mm, with postcranium; Credner 1883, pl. 12, fig. 8), 13225 (dorsal, 32 mm), 13227 (ventral, 20 mm, with anterior trunk), 13229 (dorsal, 15 mm, with almost complete postcranium; Steen 1937, fig. 4/3), 13230 (ventral side of 13562, 58 mm), 13231 (ventral, 50 mm), 13232 (dorsal, 55 mm), 13235 (dorsal, 17 mm; Boy 1989, fig. 1a), 13236 (dorsal and ventral, 16 mm), 13237 (ventral, 38 mm), 13240 (dorsal, 17 mm), 13241 (ventral, 13·5 mm),

13244+13245 (ventral and dorsal, 75 mm, with postcranium; Steen 1937, figs 2/5, 4/5, pl. 1, figs 1, 2, pl. 2, fig. 1; Boy 1989, figs 1d, 2b, 3, 4f, g), 13417 (dorsal, 15 mm, with complete postcranium), 13522+13523 (dorsal and ventral, 23 mm, with anterior trunk), 13555 (dorsal, 45 mm, with anterior trunk), 13556 (lectotype counter-slab, dorsal, 33 mm; Credner 1883, pl. 11, fig. 1), 13561 (dorsal, 20 mm), 13562 (dorsal, 58 mm), 13563 (dorsal, 30 mm), 13566+13567 (ventral and dorsal, postcranium with complete tail, fragmentary skull estimated 32 mm on the basis of comparison of the parasphenoid size with that of LFUG-13215 and 13523), 13582+13583 (dorsal and ventral, very slender skull, 32 mm).

2. Naturhistorisches Museum Chemnitz, Germany. (NHMC-F): 9887 (ventral, 26 mm).
3. Staatliches Museum für Naturkunde, Dresden, Germany. (MMG-SaP): 129 (dorsal, 37 mm), 130 (dorsal, 36 mm, with postcranial elements; Geinitz & Deichmüller 1882, pl. 7, fig. 9), 131 (dorsal, 26 mm, with postcranial elements), 132 (dorsal, 34 mm), 743 (dorsal, 38 mm, with postcranial elements). Uncatalogued: disarticulated skull with good parasphenoid (circa 30 mm).
4. Museum für Naturkunde Berlin, Germany. (MB): Am.411 (dorsal, 19 mm, with anterior trunk).

The small skeleton figured by Steen (1937, pl. 2, figs 2, 3, skull length about 15 mm) was the only previously described specimen not available to us; it is not present in any of the above-listed collections.

2. Systematic palaeontology

Temnospondyli Zittel, 1888
Zatracheidae Cope, 1882
Acanthostomatops Kuhn, 1961
Acanthostomatops vorax (Credner, 1883)

1882 *Melanerpeton spiniceps* Geinitz & Deichmüller, pp. 27–30, pl. 8, figs 8–11 partim!
1883 *Acanthostoma vorax* Credner, pp. 277–288, pl. 11, figs 1–6, pl. 12, figs 1–2.
1937 *Acanthostoma vorax* Steen, pp. 491–499, figs 1–4, pl. 1, 2.
1961 *Acanthostomatops vorax* Kuhn, p. 79.
1989 *Acanthostomatops vorax* Boy, pp. 133–151, figs 1–5.

Lectotype. LFUG-13556, skull roof, and LFUG-13214, palate (=S-285+286) (Credner 1883, pl. 11, figs 1, 2). This skull measures 33 mm.

Type horizon. Niederhäslich-Schweinsdorf Formation, Lower Rotliegend, Autunian, ? Asselian (lowermost Permian).

Type locality. Niederhäslich at Freital near Dresden, Saxony, Germany.

Referred material. In addition to the lectotype, 30 specimens have been identified as *A. vorax* and these were all examined for the present study (for complete list see Material section).

Diagnosis. Autapomorphic character-states are: (1) lacrimal and prefrontal project into orbit, (2) quadratojugal with two large lateral spikes and angular with five ventral spikes, (3) interclavicle transversely rectangular and very small, reaching less than half the area of the parasphenoid plate, (4) humerus large and solid from small size on, longer than femur in larger specimens. Characters shared with other temnospondyls: (1) postorbital skull table abbreviated with supratemporals, parietals, and postparietals being especially short; (2) choana laterally constricted by fang bases; (3) pronounced muscular pockets at posterolateral rim of parasphenpoid plate; (4) deltoid denticle field on base of parasphenoid process and plate; (5) 21–22 presacral vertebrae; (6) humerus with supinator; (7) trunk only 1.6 times longer than skull in adults.

***Non* Acanthostomatops.** The specimen Werneburg (1998, p. 50, figs 1–3) described as a larval specimen of *A. vorax* is actually a medium-sized individual of the micromelerpetontid dissorophoid *Branchierpeton amblystomum* (Credner 1881). In addition to lacking all autapomorphies of *A. vorax*, this small specimen (17 mm skull length) has a different snout morphology and an elongated posterior skull table, the latter being a synapomorphy of micromelerpetontids. Examination of the counterpart of Werneburg's (1998, fig. 1) specimen revealed that there is no internasal fontanelle and that the preorbital region is substantially shorter than in *Acanthostomatops*. Apparently, Werneburg interpreted a fracture in the nasal as the rim of the internasal fontanelle. Likewise, the interclavicle and cleithrum are quite different from those of *Acanthostomatops*, and in the latter the presence of ossified vertebral centra is not observed in specimens smaller than 75 mm skull length. The present authors further agree with Credner (1883, p. 278) in that the isolated postcrania described and figured by Geinitz & Deichmüller (1882, pl. 7, figs 6, 7) as *A. vorax* (*Melanerpeton spiniceps*) are to be referred to *Onchiodon labyrinthicus*.

3. Description

3.1. General outline of the skull

Geinitz & Deichmüller (1882), Credner (1883), Steen (1937) and most notably Boy (1989) have described many aspects of the skeleton in *Acanthostomatops vorax*. Throughout these studies, the adult skull formed the focus of interest, although Boy (1989) listed various ontogenetic changes and reconstructed skulls of different size. He was the first to notice and characterise distinct morphs, coined by him 'narrow skull' and 'wide skull', respectively. The interorbital width, measuring the shortest distance between the orbits, varies particularly in *Acanthostomatops*. The present authors' measurements do not unequivocally reveal such a dimorphic distribution, as the sample of 12 analysed specimens is simply too small (Fig. 1B, C). In our view, the analyzed distribution of morphometric parameters does not confirm a simple dimorphism – to name just the most obvious: jugal width, snout width, snout length, interorbital width, squamosal length, and the shape and size of the internasal fontanelle are all very variable even across this small sample. Boy (1989, p. 139) already highlighted the limited use of the concept of dimorphism by referring to some inconsistent character distributions.

In the case of the ratio of interorbital width against skull length (Fig. 1B), the small specimens (15–38 mm skull length) appear the least variable, plotting within a narrow zone around the 0·2 level. In larger specimens greater than 38 mm, values between 0·18 and 0·3 are reached. Apparently, there was no allometric trend of this parameter at all, although some dimorphism in large specimens cannot be ruled out. The length of the snout (preorbital region) as measured against skull length is also subject to variation (Fig. 1C), but generally increased slightly with age.

3.2. Skull roof

In the present study, we focus on the cranial morphology of the smallest specimens and the developmental changes in *Acanthostomatops vorax*. The most conspicuous feature is the large preorbital region and the poor degree of allometry of most cranial traits (Fig. 2). In small specimens, the preorbital region roughly matches the length of orbits and postorbital skull table combined. The ratio of preorbital length to skull

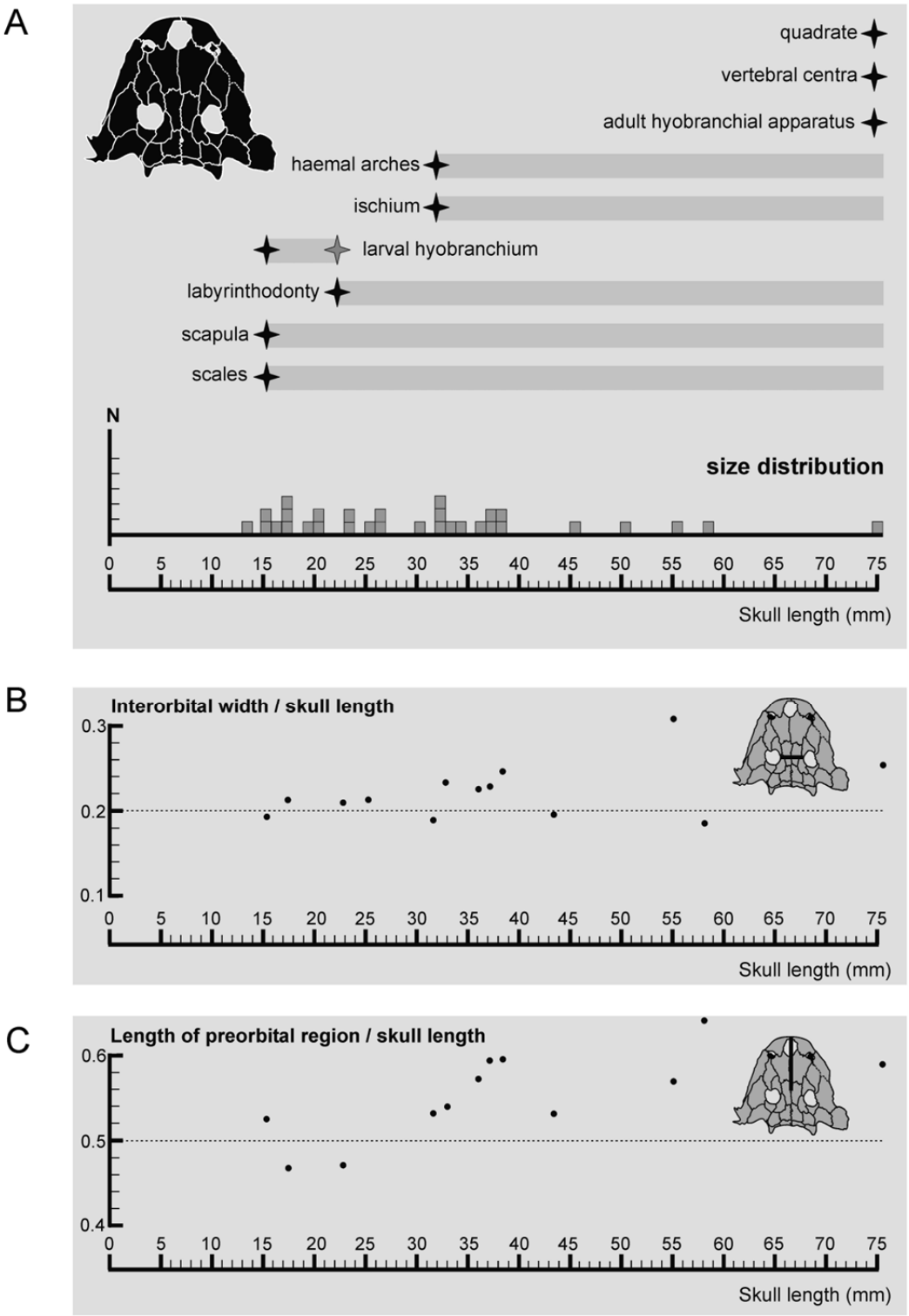

Figure 1 *Acanthostomatops vorax*. (A) size frequency distribution: number of investigated specimens (y axis) mapped against skull length (x axis) and chronology of developmental events (a black asterisk represents first appearance of an ossified element in ontogeny, whereas a grey asterisk marks its last appearance, due to resorption); (B) ratio of interorbital width against skull length (y axis) plotted against skull length (x-axis); (C) ratio of preorbital length against skull length (y axis) plotted against skull length (x-axis).

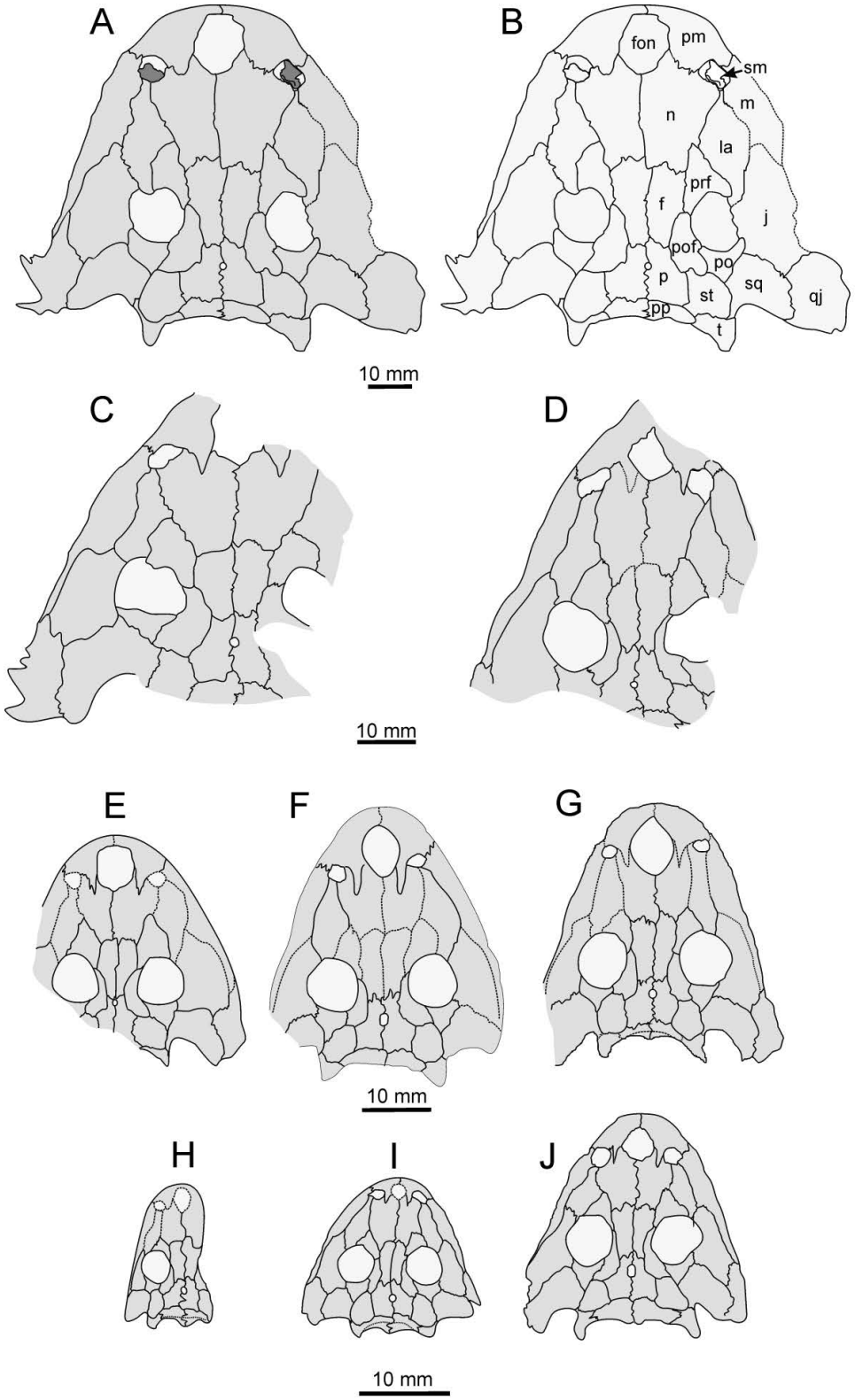

Figure 2 *Acanthostomatops vorax*. Dermal skull roofs of differently sized specimens in dorsal view: (A), (B) LFUG-13245, 75 mm; (C) LFUG-13232, 55 mm; (D) LFUG-13562, 58 mm; (E) LFUG-13556, 33 mm; (F) MMG-SaP-129, 37 mm; (G) MMG-SaP-130, 36 mm; (H) LFUG-13417, 15 mm; (I) LFUG-13235, 17 mm; (J) LFUG-13522, 23 mm.

length ranges from 0·47 in the smallest specimens to 0·64 in large individuals (Fig. 1C). The best-preserved small specimen (LFUG-13417) has a snout-to-skull ratio of 0·52. In this, larvae of *Acanthostomatops* are clearly unique among temnospondyls in having a long snout region from a small size upwards.

3.2.1. Preorbital region. In the smallest larval specimens, the preorbital region already reaches 1·6 to 1·8 times the length of the posterior skull table. This is much higher than in similar-sized larvae of other temnospondyls (*Sclerocephalus*: 0·8–1·3, *Onchiodon*: 1·0–1·2, observation by the present authors). Likewise, the nasal and lacrimal of small *Acanthostomatops* have nearly adult proportions, while the premaxilla experienced a substantial positive allometry within the 23–35 mm range. The same applies to the dorsal internasal fontanelle, which is proportionally largest in slender-skulled specimens.

3.2.2. Skull table and cheek. In general, small skulls already have strongly asymmetrical sutures. For instance, the medial suture between the parietals is strongly serrated. The supratemporal is narrow in 15–20 mm specimens, having an elongated rectangular outline (Fig. 3A, B). In slightly larger skulls (from 23 mm on), the posteromedial part has become wider, constricting the parietal posterolaterally (Fig. 3C). In the large adults, the supratemporal covers an almost quadrangular area, having an irregular outline (Fig. 3D). The parietal is proportionally narrower in the 15–17 mm skulls, with its posterior half being narrower than the anterior one. The postorbital is pointed, forming a near-perfect triangle; in larger specimens, it has more rounded margins and only a faintly pointed end. The prefrontal does not clearly reach the postfrontal in the tiny specimen (LFUG-13417; Fig. 3A), but does so in all larger specimens. Likewise, the anterior portion of the jugal forms only a slender process in 13–17 mm skulls. LFUG-13417 further differs from all others in having a squamosal that does not reach the tabular on the dorsal side; this feature develops slowly with larger size, being most clearly established in adults.

3.2.3. Length of gape. The length and posterior extension of the squamosal and quadratojugal varies in small larvae. While in the 15 mm skull LFUG-13417 the supposedly more mature condition is established with the squamosal at least at the same level as the postparietal (Fig. 3A), the 17 mm LFUG-13235 and the 23 mm LFUG-13522 (Figs 2I, J, 3B, C) have abbreviated squamosals ending level with the parietal-postparietal suture. This may indicate differences in feeding, as the former specimen has a proportionally longer gape. However, this is far from clear as long as a concomittant dimorphism in dentition has not been proven. Variation in gape length persists in large specimens (55 and 58 mm skull length), whilst the 75 mm LFUG-13244+45 has a remarkably short gape (Figs 3D, 4). A proportionally longer gape is mostly found in specimens with narrower preorbital regions, more slender jugals, and narrower interorbital regions and may be correlated. Yet the specimen with the widest skull (LFUG-13232; Fig. 2C) has a quadrate with the most posterior position of the entire sample.

3.2.4. Occipital flange. The smallest specimens have a single and medial, well-developed occipital flange (Fig. 3A–C) that is proportionally larger than in adults – in the small larvae it is even larger than the ornamented part of the bone. In large specimens, the flange descends ventrally, often only visible in ventrally exposed skulls.

3.2.5. Otic notch. A tabular horn is developed from a small size on, in larger specimens forming the bulk of the element (Figs 2, 3). Although it does not reach the length it attains in *Zatrachys* (Schoch 1997), the horn is still larger than in many other temnospondyls. It is peculiar in being ornamented not only on top, but also along the entire lateral flank, suggesting that skin reached well down into the otic notch region. This implies that the tympanum – assuming that it was present – must have attached to the frame of the otic notch in a different fashion than was supposedly the case in other temnospondyls (Bolt & Lombard 1985), with two alternatives emerging: either (i) the tympanum was embedded more deeply within the notch, much below the level of the skull table, or (ii) it was slit-like, restricted to the squamosal margin, and not reaching the tabular attached to some unknown and unpreserved structure. The latter possibility is suggested by the fact that the squamosal does not have a downcurved ornamented area, as would be expected if the tympanum was located at a much deeper level. The present authors thank Andrew Milner for drawing our attention to this feature. Ventrally, the tabular bears a deep socket for the attachment of the parotic process (Fig. 4), which remained unossified throughout all samples.

3.2.6. Sclerotic ring. Ossified platelets of the sclerotic ring are present even in the smallest complete specimen, there being at least ten elements (LFUG-13417; Fig. 3A); there are no palpebral ossicles as in some dissorophoids of similar size. The medial plates at the postfrontal–prefrontal margin are large and rectangular, whereas the lateral and anterior plates are tiny and quadrangular. In the 58 mm skull LFUG-13562, two lateral plates of the sclerotic ring are exposed in the left orbit, revealing the presence of such a ring also in large *Acanthostomatops*. In most specimens larger than 20 mm skull length sclerotic plates are not observed, but it is possible that they are obscured by sediment.

3.3. Palate

3.3.1. Palatal ossicles. The lectotype preserves numerous tiny, tooth-bearing palatal ossicles similar to those known from many temnospondyls, e.g. *Adamanterpeton* (Milner & Sequeira 1998), *Platyrhinops* (Carroll 1964; Clack & Milner 1994), *Uranocentrodon* (van Hoepen 1915), and trematosaurids (Schoch 2006). In another specimen (LFUG-13523) palatal ossicles are especially numerous and quite large, obviously having covered the interpterygoid vacuities. The tiny teeth attached to them are similar in morphology to those of the pterygoid and vomer. In the 38 mm skull MMG-Sap-743, large palatal ossicles are present at the periphery of the anterior palatal fontanelle, whilst in the 75 mm LFUG-13245 most of the dentigerous palatal ossicles are unusually tiny (Fig. 4).

3.3.2. Parasphenoid. This bone underwent an interesting ontogeny and shows extensive individual variation (Fig. 5B–G). In a 20 mm skull (LFUG-13227; Fig. 5E) the parasphenoid is dominated by a large deltoid denticle field that occupies the entire centre of the parasphenoid plate and continues far onto the cultriform process. The posterolateral corners of that field are pointed and merge into small posterolateral wings, recalling the situation in *Lydekkerina* (Shishkin *et al.* 1996), and the posterior margin of the tooth patch is markedly concave. The parasphenoid plate still lacks the prominent muscular pockets of those from larger size classes, although the small posterolateral wings may well form the lateral margins of such muscle attachments. The basipterygoid processes are simple yet prominent, attaching by means of an overlapping suture to the medial rami of the pterygoids. The denticle field is clearly set off from the basipterygoid processes by grooves parallel to the margin of the field. In LFUG-13215 (25 mm skull length; Fig. 5F) and a similar-sized, disarticulated specimen (MMG-SaP uncatalogued), the denticle field is smaller and more restricted to the anterior part of the parasphenoid plate. In these and larger specimens, the outline of the denticle field varies from broad deltoid with pointed lateral ends to narrow with

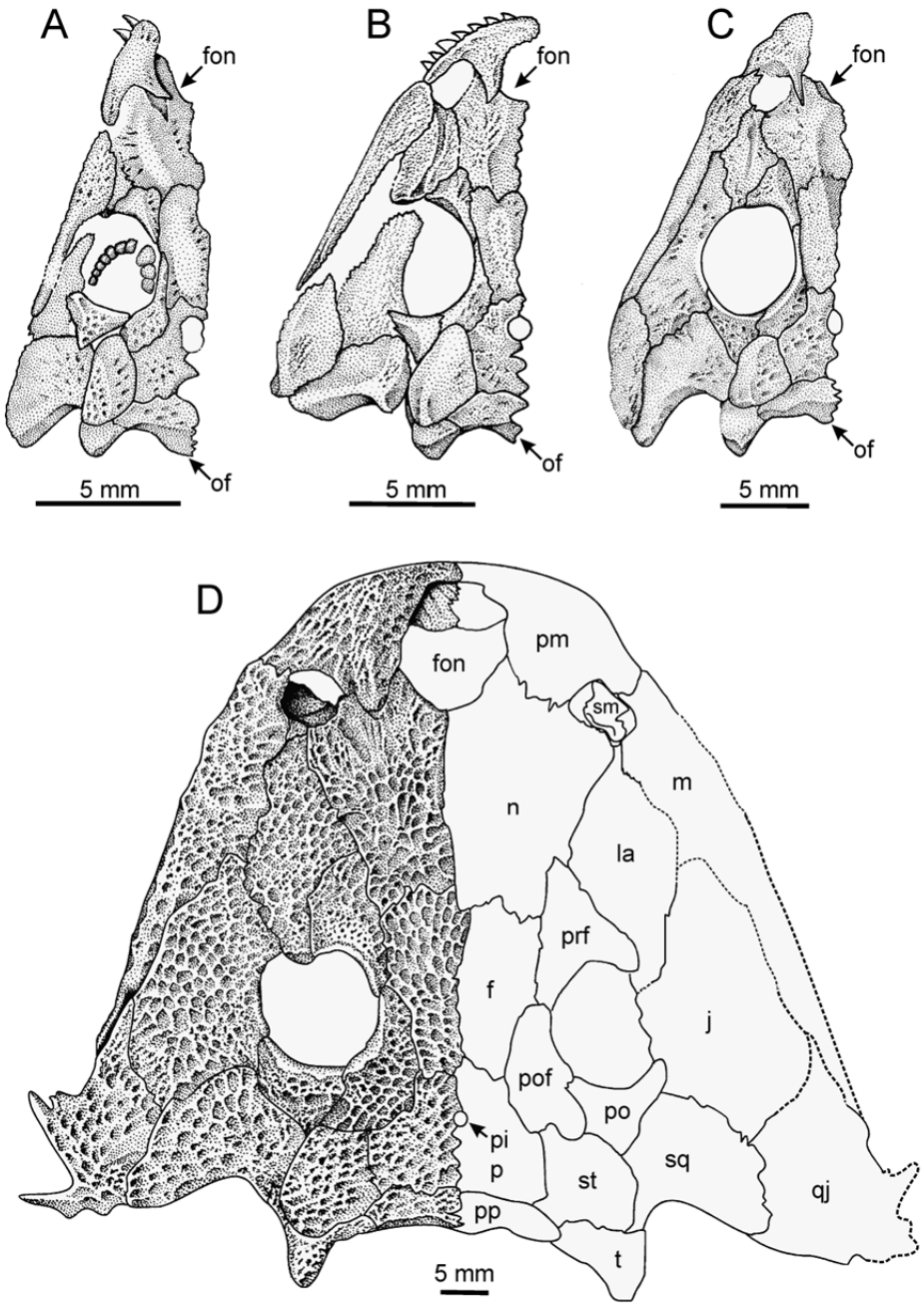

Figure 3 *Acanthostomatops vorax*. Sculptural development of the dermal skull roof: (A) LFUG-13417, 15 mm; (B) LFUG-13235, 17 mm; (C) LFUG-13522, 23 mm; (D) LFUG-13245, 75 mm.

rounded posterior margin and not set off from the anterior part emplaced on the cultriform process. The best-preserved parasphenoid is that of LFUG-13566+13567, where the element is completely exposed from both ventral and dorsal sides (Fig. 5C, D). The denticle field is laterally framed by shallow grooves, and in LFUG-13566 there is a small opening on both sides, not far from the anterior margin of the parasphenoid plate. These openings appear to be exit foramina for the internal carotid artery, as described by Boy (1989). It is striking that this configuration is unequivocally present in only two specimens (LFUG-13214, 13566), while many others appear to lack openings altogether. Entrance foramina, as postulated by Boy (1989), are not preserved, but may have been located in the posterolateral corners of the parasphenoid plate, probably on the dorsal side. In large specimens (e.g. LFUG-13244), the muscular attachments in the posterolateral corners have become very pronounced, with the anterior margin clear-cut and forming true pockets (Figs 4, 5B). In the anteromedial portion of the dorsal side of the parasphenoid plate of LFUG-13567, a small rectangular area is preserved which is

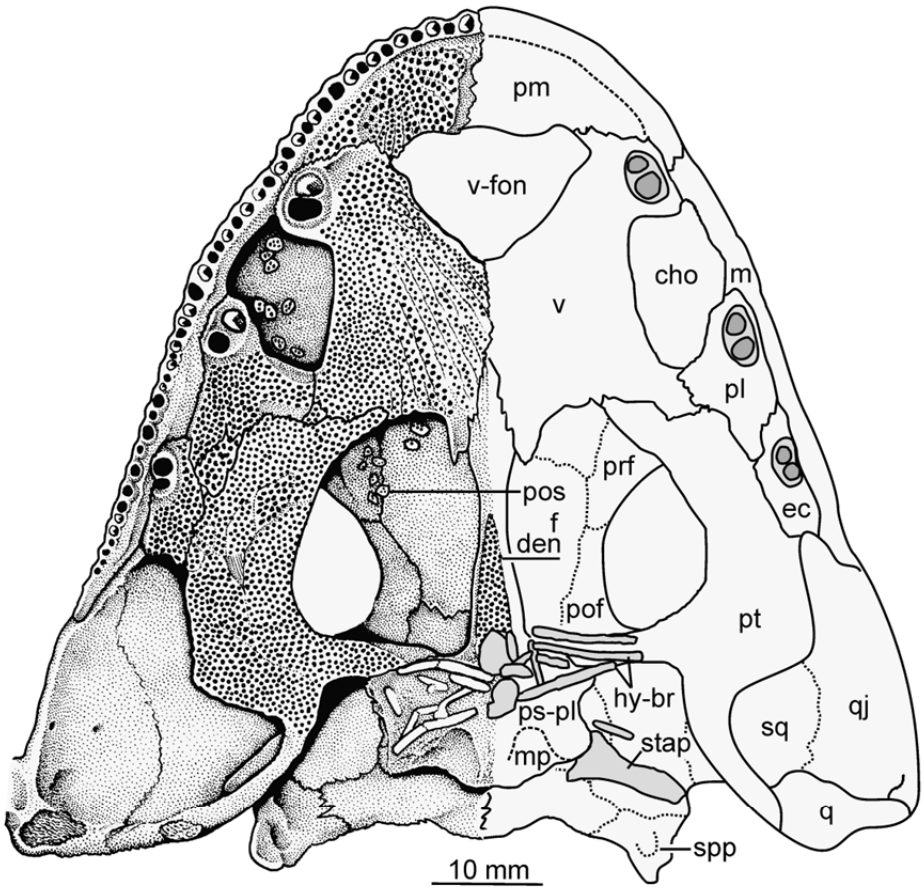

Figure 4 *Acanthostomatops vorax*. Palate of the largest specimen LFUG-13244 (75 mm) with ossified hypobranchials and stapes.

slightly raised and has a rugose surface (Fig. 5D). Similar structures are known from *Dvinosaurus* (Shishkin 1973) and *Apateon* (Boy 1972), where they have been termed *crista sellaris* and interpreted as a facet for an articulation with the basisphenoid cartilage formed by the parasphenoid. From this elevated area, the parapterygoid crest (*crista parapterygoidea* of Bystrow & Efremov 1940) runs posterolaterally. It was found to have served as site of attachment for the ventral process of the stapes (see below) in several temnospondyls, such as *Aphaneramma* (Säve-Söderbergh 1936), *Lyrocephaliscus* (Mazin & Janvier 1983), and *Mastodonsaurus* (Schoch 2000). The crest is separated from the shallower, almost anteroposteriorly-oriented paroccipital crest (*crista paroccipitalis*) by a broad furrow, the *sulcus intercristatus* of Bystrow & Efremov (1940). The shallow basioccipital fossa (fossa basioccipitalis) is situated between the left and right part of the paroccipital crest.

3.3.3. Pterygoid, ectopterygoid, palatine, vomer. The marginal series of palatal elements is characterised by large, dentigerous areas (Fig. 4). The teeth are uniform, tiny, and closely set. On the vomer, which houses the most extensive of these tooth-patches, teeth are arranged in radial rows converging towards a point near the vomerine fang pair. These rows are separated by grooves. On the palatine and ectopterygoid, the rows are less clear but exist, while on the pterygoid the arrangement of groups of denticles follows a more reticulate pattern. The fangs are labyrinthodont with marked infolding at their bases, and are markedly curved with the crowns pointing both buccally and posteriorly. Labyrinthodonty is first apparent in skulls of 22 mm size (LFUG-13070).

The pterygoid has a well-ossified and large ascending lamella (LFUG-13567), which must have formed a completely or largely closed occipital surface in the cheek region. In the pterygoid, the entire surface of the ventrally exposed parts is covered with teeth. The basipterygoid ramus becomes only slightly proportionally longer in large specimens, adding little to the greater width of adult skulls. In contrast to almost all other temnospondyl larvae, this ramus is well ossified from the smallest sizes, eventually forming a complete facet for the basipterygoid articulation. Likewise, the palatine ramus is broad and firmly sutured with both the palatine and vomer, completely separating the interpterygoid vacuities from the palatine and ectopterygoid. In large specimens, the palatine ramus is proportionally nearly twice as wide as in small ones. Similarly, palatine and ectopterygoid experienced little changes during ontogeny, becoming somewhat wider, as in *Onchiodon* (Boy 1990) and unlike *Sclerocephalus* (Boy 1988; Schoch 2003). The medial process of the palatine, which is broadly sutured with the vomer, is twice as wide in adults compared to small larvae. Unlike in many other temnospondyls, the morphology of the vomer, anterior palatal fontanelle, and the choana is remarkably constant through ontogeny.

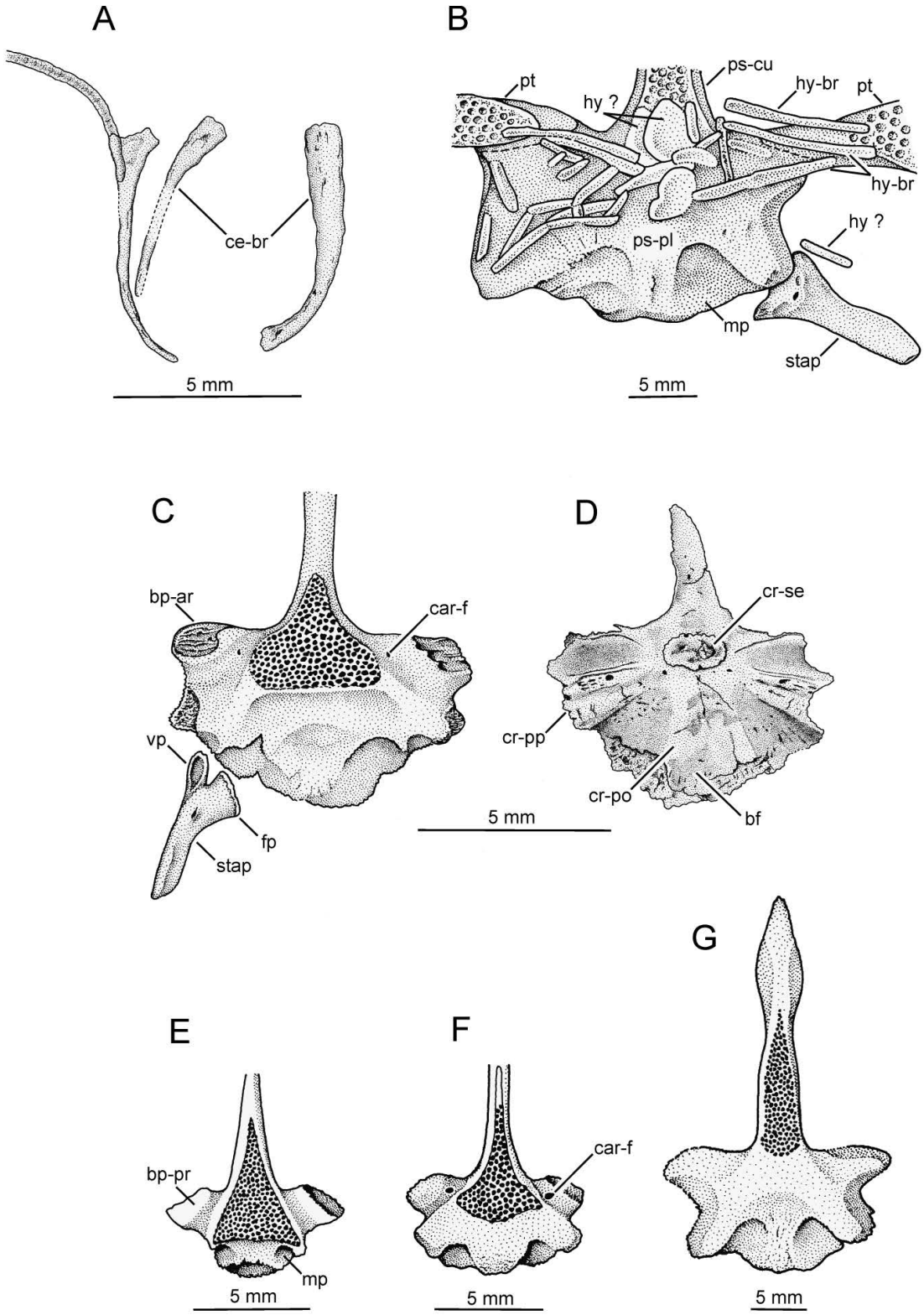

Figure 5 *Acanthostomatops vorax*. (A), (B) hyobranchial elements: (A) ossified ceratobranchials of the larval specimen LFUG-13070, 22 mm; (B) ossified hypobranchials on the ventral side of the parasphenoid plate in LFUG-13244 (75 mm). (C)–(G) parasphenoids of differently sized specimens: (C) LFUG-13566, circa 32 mm, ventral, with stapes; (D) LFUG-13567, dorsal; (E) LFUG-13227, 20 mm, ventral; (F) LFUG-13215, 25 mm, ventral; (G) LFUG-13244, partially restored, 75 mm, ventral.

3.4. Endocranium

The braincase and palatoquadrate regions remained to a large extent unossified throughout the size classes studied. There is no trace of a bony sphenethmoid, basisphenoid, basioccipital, exoccipital or epipterygoid at any stage. The only element that can be unequivocally confirmed is the quadrate, which is present as a distinct ossification only in the largest specimen (LFUG-13244, Fig. 4). This corresponds well with the presence of an articular bone in the mandible of the same specimen. The absence of an ossified exoccipital is particularly remarkable, as this element was the first to appear in the sequence of braincase elements in many temnospondyls (Bystrow & Efremov 1940; Boy 1995; Witzmann 2005), and is even present in large specimens of more aquatic taxa such as *Sclerocephalus* (personal observation by present authors) or *Trimerorhachis* (Case 1935). The posterolateral margins of the parasphenoid plate have two prominent rugose areas with upcurved margins that probably attached to the exoccipital region, which remained cartilaginous. In contrast, the basioccipital region (basioccipital fossa) is smooth and probably did not house a large basioccipital cartilage; this is weak evidence for the existence of a two-headed, medially separate occipital articulation. Except for the facet for the basisphenoid cartilage formed by the parasphenoid, no ossified part of the basisphenoid itself is visible.

3.5. Visceral apparatus

3.5.1. Hyobranchial skeleton. In *Acanthostomatops vorax*, various ossified elements of the hyobranchial apparatus are preserved in small specimens as well as in the largest known skull. As the small and large specimens differ conspicuously in the structure and composition of the hyobranchium, we describe them in separate sections.

Small specimens. Steen (1937) described three pairs of ossified branchial arches in the smallest specimen studied ('specimen A', skull length about 15 mm). Morphology and position of these structures indicate that they represent ceratobranchials. According to Steen's (1937) photographs (pl. 2, figs 2, 3), there might also be a fourth arch present on the left side. The present authors also found three bony bars on the left side posterior to the 22 mm long skull of LFUG 13070 (Fig. 5A). The medial end is greatly expanded and flattened, whereas the curved shaft is slender and rounded in cross section. Posterolateral to the left orbit, a fourth bar is present which is curved and of similar length to the posterior bars, but is much more robust. It is possible that this bar represents the first ceratobranchial, and the succeeding arches become increasingly more slender posteriorly, resembling the situation in *Dvinosaurus* (Bystrow 1938) and *Trimerorhachis* (Olson 1979). Alternatively, the broader arch could represent a ceratohyal. With the exception of the narrow posteriormost element that has a rugose bony structure, the ceratobranchials have a largely smooth surface and are better ossified in *Acanthostomatops* than in larval *Onchiodon* (Witzmann 2005). As Steen (1937) and Boy (1989) noted, the hyobranchial apparatus of *Acanthostomatops* lacks branchial dentition, and there is no ossified basibranchial.

Largest specimen. In the palate of LFUG-13244 (75 mm skull length), the ventral surface of the parasphenoid plate is covered by six elongate bony rods and several smaller, less clearly defined elements (Fig. 5B). Most of these bones have a spongy structure. The largest elements are relatively long and thin, being only very gently curved. On either side, at least three rods of similar size are present, arranged in an anteroposterior sequence. The arrangement of these numerous bones resembles most closely the hyobranchium of lysorophians (Wellstead 1991). On the right side of the parasphenoid plate (ventral view), three slender, simple bars are preserved, each of them being longer than half the width of the parasphenoid plate. The anterior two are parallel and directed anteromedially, whereas the third is aligned posteromedially; this is obviously the result of disarticulation. On the left side, at least three similar elements are present, albeit more fragmentary and disarticulated.

Apart from the long bars, several short bones are present that are largely anteroposteriorly aligned. In addition to the bony rods described, at least four plate-like bones are preserved in the centre of the parasphenoid plate and at the base of the cultriform process. It is not clear if these structures also belong to the hyobranchial apparatus.

3.5.2. Stapes. In LFUG-13566, the complete right stapes is preserved near the posterolateral margin of the parasphenoid plate, very close to its probable articulation at the parapterygoid crest (Fig. 5C). The stapes of this specimen is about as long as the parasphenoid plate, having a straight shaft and a differentiated proximal head. The latter is clearly bipartite, with a long ventral process and a wide footplate. The general morphology of the stapes matches that of *Eryops* (Sushkin 1927; Sawin 1941), *Trimerorhachis* (Bolt & Lombard 1985) and *Mastodonsaurus* (Schoch 2000). The ventral process bears a notch suggesting some kind of articulation with the parapterygoid crest of the parasphenoid. At some distance from the bifurcation, the shaft bears a slit-like opening supposedly for the stapedial artery. The short and straight shaft has a uniform width throughout the distal half and bears a ridge along the antero-medial side, paralleling the long axis of the shaft. The stapes is shorter than in most stereospondyls and the larger eryopoid-grade temnospondyls, but is clearly longer and more differentiated than in the dissorophoids *Doleserpeton* (Bolt & Lombard 1985), *Amphibamus* (Daly 1994), and *Micromelerpeton* (Boy 1995).

In addition, the ventral side of the adult skull LFUG-13244 preserves the stapes on the right side in ventral view (Figs. 4, 5B). The head region is partly obscured by the underplating parasphenoid plate, but it is consistent with that of LFUG-13566 in becoming wider towards the proximal end. The existence of a separate ventral process is indicated by a groove between the ventral (posterior) part of the proximal region and the footplate proper. A stapedial foramen is also present close to the bifurcation, being somewhat larger than in LFUG-13566.

Boy (1989, p. 143, fig. 4a) described and figured a stapes-like element in a 58 mm skull (LFUG-13562) located in isolation within the right orbit. Although more ambiguous than LFUG-13566, this bonelet may well form part of a stapes, preserving only the proximal head region and a small portion of the medial shaft. A large pit or opening near the 'head' of that element resembles the stapedial foramen in location and shape, although its exact size is obscured by sediment. The main difference between this fragmentary element and the complete stapes in LFUG-13566 is the undivided, simple 'head' region, which with the now available evidence may now be interpreted as incomplete.

3.6. Mandible

The mandible was described in detail by Boy (1989), who also provided a reconstruction of the adult condition. The present authors add only a short note on one point where they came to a different conclusion, namely the existence of a Meckelian window. They found some evidence for such a window in the outline on the angular in LFUG-13245, which has a pronounced concave recess along its anterodorsal margin. The height of this window is unclear due to the disarticulation of the angular, but its posterior and ventral margins are well

preserved. The minimal length of the Meckelian window can therefore be assessed, and reaches about one sixth of the total length of the mandible. In addition, the articular makes its appearance only in the largest specimen (LFUG-13245) as a coarse-grained bone of roughly quadrangular shape; the articular facet is well-established, and the bone extends ventrally and anteriorly along the internal surface of the angular and surangular, respectively.

3.7. Postcranial skeleton

Only a few specimens include parts of the postcranium, although it appears that most material was originally deposited in articulated state. However, as the postcranial elements of *Acanthostomatops* are mostly feebly ossified, it is obvious that the focus of collecting at Niederhäslich was on skulls. A similar collection bias was reported by Boy (1990). In addition to Steen's (1937) and Boy's (1989) observations on the postcranium, which were both rather cursory, the present authors have examined all available material with particular emphasis on the tail skeleton, girdles, and limbs. Boy (1989) in particular based most of his description on the largest individual (LFUG-13244+45), whereas the present authors have recognised a full range of fragmentary specimens that add information both on the ontogeny and the anatomy of various postcranial elements, permitting a quite complete skeletal restoration of *Acanthostomatops*.

3.7.1. Axial skeleton. *Acanthostomatops* has a rather short trunk composed of 21–22 presacral vertebrae. In combination with the abbreviated tail, this small-growing zatracheid was short-built with a disproportionally large skull. In the small larva LFUG-13229, the ratio trunk to skull length is 1·9, whereas in the largest specimen (LFUG 13244+45), it is 1·6.

Neural arches of the trunk. As is common among larval temnospondyls (e.g. Boy 1974), specimens smaller than 20 mm skull length have still separate and poorly ossified neural arches (LFUG-13417, 13221, 13229, MB.Am.411). The neural spines are very low and form a slightly convex dorsal margin above the rudimentarily developed zygapophyses (Fig. 6A, B). The ventral portion of the neural arches is slender and lacks transverse processes. In specimens of 20–35 mm range, neural arches are still poorly ossified but the neural spines are proportionally slightly higher (LFUG-13522, 13523, 13566, MMG-SaP-131). Three-dimensionally preserved neural arches have inwardly curved anterior and posterior margins wrapping around the medial surface but failing to meet each other medially (Figs 6C, D, 7). They probably represent primordia of perichondral bone formation enclosing a cartilaginous core.

In LFUG-13244+45, most parts of the presacral vertebral column are exposed (Figs 8, 9A, B). The neural spines are robust and relatively low, although markedly higher than figured by Boy (1989, fig. 4b). Their dorsal portion is thickened with a rugose surface on top, a feature present at least in the posterior half of the column. Whereas the postzygapophyses form ill-defined depressions at the posterior base of the neural spine, the prezygapophyses are large and well developed. Their unfinished articulation surfaces face dorsomedially and anteriorly. The neural canal is not exposed in any of the neural arches and it cannot be determined if it was open or closed ventrally. With respect to the width of the neural arch, the neural spine is broad in anterior view. In the mid-trunk region, the angle between the transverse process and the neural spine is slightly higher than 100°, if seen in anterior view. When viewed dorsally, the transverse process is aligned at approximately right angles to the central portion of the neural arch, so that the anteroposteriorly elongated diapophysis faces laterally and slightly ventrally. However, these measurements cannot be taken in other regions of the vertebral column because of crushing of the neural spines and the transverse processes.

Atlas and axis. The anteriormost vertebrae are scarcely preserved, and atlas and axis cannot be determined with certainty because of the poor state of preservation. The first three neural arches seem to be more slender than the posterior ones (LFUG-13417; Fig. 6A). In LFUG-13522 (Fig. 6C), the first three or four neural arches are smaller than the succeeding arches; small, paired bony elements posteroventral to the occipital flange of the postparietals might represent components of the proatlas in this specimen.

Intercentra. The slender, wedge-shaped structures in LFUG-13229 described as intercentra by Steen (1937, fig. 3) are actually parts of the pectoral girdle. According to the present authors' findings, only the largest specimen (LFUG-13244+45) preserves unequivocal ossified inter- and pleurocentra (Figs 8, 9A). They are well-ossified throughout. As centra were still unossified in a 45 mm skull (LFUG-13555), their formation must have started in specimens within the 45–75 mm range. As described by Boy (1989), the unpaired intercentra are large and have a mostly smooth outer surface without parapophyses. In lateral view, each of the trunk intercentra is anteroposteriorly elongated with a blunt-ending flank (ascending process). The cross-section of an intercentrum shows that it is strikingly thin, leaving a large space for the unrestricted notochord, similar to the thin-walled intercentra of the basal temnospondyl *Dendrerpeton acadianum* (Holmes *et al.* 1998). The dorso-medial side of the intercentra is coarsely rugose.

Pleurocentra. As in *Dendrerpeton* (Holmes *et al.* 1998) and *Zatrachys* (Langston 1953), the paired pleurocentra are more massive than the intercentra. They also form wedge-shaped elements with the dorsal portion being broader than the tapering ventral part. As described by Steen (1937) and Boy (1989), both lateral and medial surfaces are roughened (Figs 8, 9A). The pleurocentra extend far ventrally almost towards the ventral midline, similar to dissorophoids (Boy 1985, 1995), as well as trimerorhachids and saurerpetontids (Chase 1965; Hotton 1959). In the available material, the pleurocentra seem to become more slender and shorter caudally in the trunk. A similar condition, in which the pleurocentra become more restricted in the posterior part of the trunk, is found in *Dendrerpeton* (Holmes *et al.*1998).

Caudal vertebral column. The almost complete tail of *Acanthostomatops* is preserved in LFUG-13566+67, on which the following description is based (Fig. 7). The tail is proportionally short and consists of only 28 vertebrae. In that region, the neural arches bear very low spines that are more slender than in the trunk. The size of the neural arches decreases rapidly towards the end, with the posteriormost arches subquadrangular in outline. Haemal arches are stout and distally not fused, and are therefore difficult to distinguish from the caudal rib series. The fifth caudal vertebra is the last one with ribs and the first one with haemal arches in the vertebral column. All succeeding vertebrae have haemal arches but lack centra. LFUG-13566+67 reveals that the haemal arches started to ossify prior to the centra, a pattern also present in *Micromelerpeton credneri* (personal observation by the present authors).

Ribs. Ribs are rarely preserved, and there is no specimen with a complete series of ribs. It is unclear whether the atlas or axis bore the first rib. The first two ribs are short and slender whereas the following ones are distinctly broadened at both ends, a consistent feature of both small and large specimens (Figs 6A, C, 9C, D). During ontogeny, the ribs of the trunk become proportionally longer. The proximal end is single-headed, as Langston (1953, fig. 16d) described for *Zatrachys*

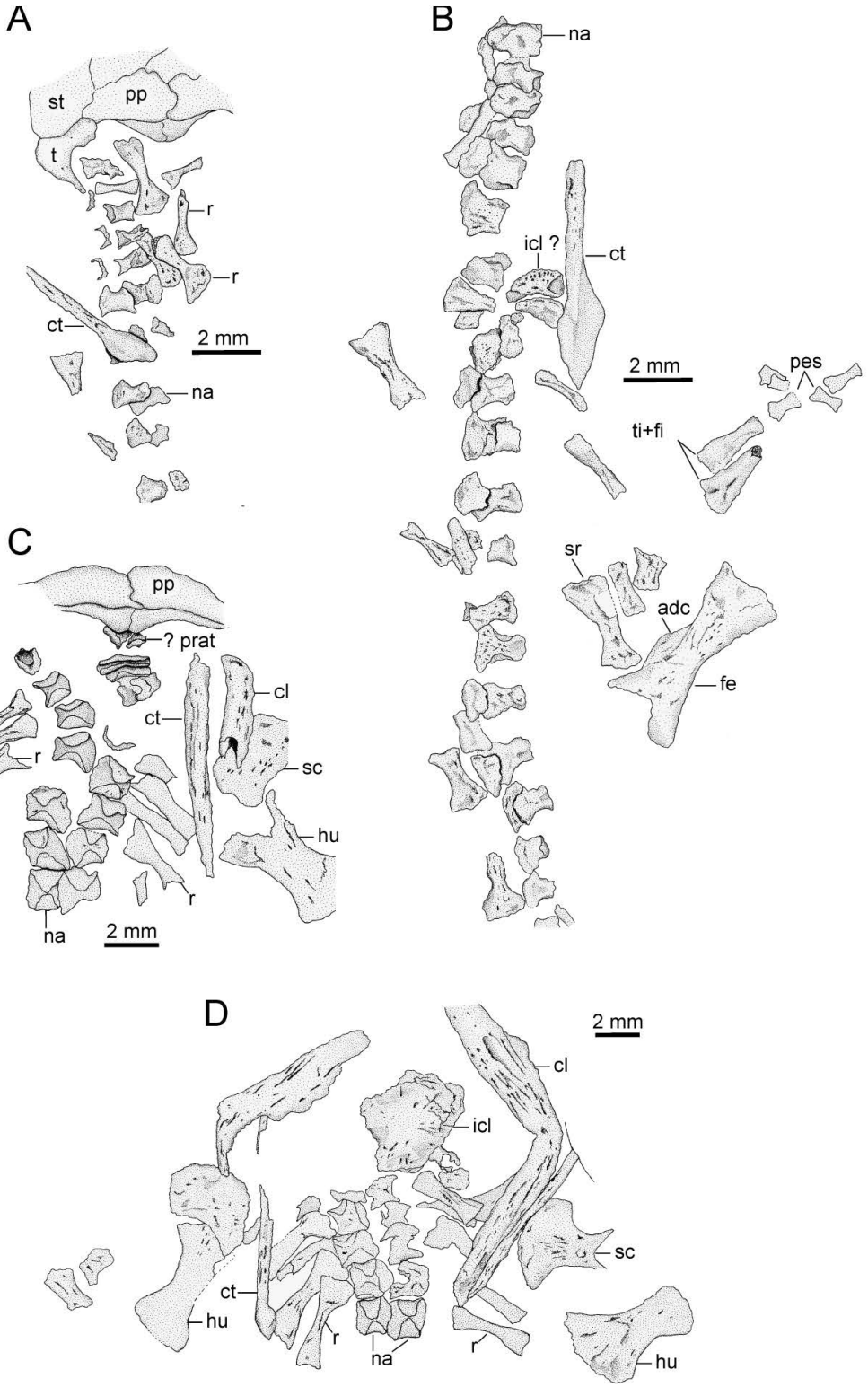

Figure 6 *Acanthostomatops vorax*. Postcranial larval skeletons: (A) LFUG-13417, 15 mm, dorsal; (B) LFUG-13229, 15 mm, dorsal; (C) LFUG-13522, 23 mm, dorsal; (D) LFUG-13523, 23 mm, ventral.

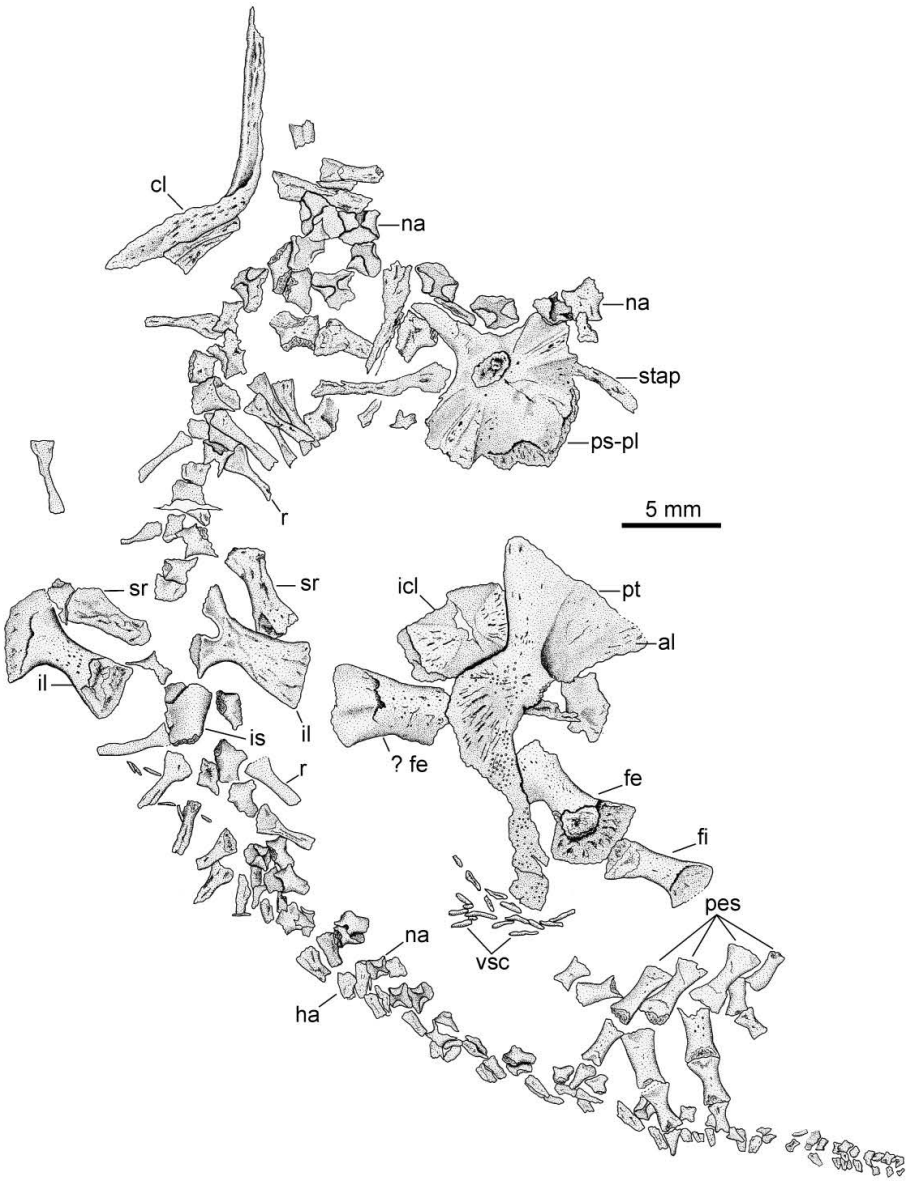

Figure 7 *Acanthostomatops vorax*. LFUG-13567, circa 32 mm, dorsal, postcranial skeleton with complete tail and fragments of pectoral and pelvic girdle, hindlimb, and palate.

serratus. As in the latter taxon, there are no uncinate processes. The ribs of the posterior trunk are slender and become shorter caudally (Fig. 9E). In one of the smallest specimens (LFUG-13229), the sacral rib is already differentiated with a stout proximal head and a considerably expanded distal end (Fig. 6B). In LFUG-13566+67 it is more robust with a proportionally broader shaft (Fig. 7), and in LFUG-13245 the expanded distal end has almost three times the width of the shaft (Fig. 9F), reaching proportions comparable to the massive sacral rib of *Eoscopus lockardi* (Daly 1994, fig. 10). As reported, the first five caudal vertebrae have short ribs with a broadened head and a slender shaft (Fig. 7).

3.7.2. Pectoral girdle. In its general outline, the pectoral girdle of *Acanthostomatops* is very slender. It includes the standard complement of bones: interclavicle, clavicles, cleithra, and incompletely ossified scapulocoracoids.

Interclavicle. Fragments of the interclavicle are probably visible in LFUG-13229 (Fig. 6 B), and this unusually small element is well preserved in only three specimens (LFUG-13227, 13523, 13566+67; Figs 6D, 7, 10A–C). Nothing is known of the later ontogeny of the interclavicle in specimens beyond 32 mm skull length. The area it covers is even smaller than half the parasphenoid plate (LFUG-13566+67). It is transversely rectangular, with unclear margins. In contrast to Boy (1989, fig. 5a), the present authors consider the convex margin to be the posterior one, and the almost straight edge being anterior (Fig. 10A, B). This is based on LFUG-13523 and 13227 in which the orientation of the interclavicle can be

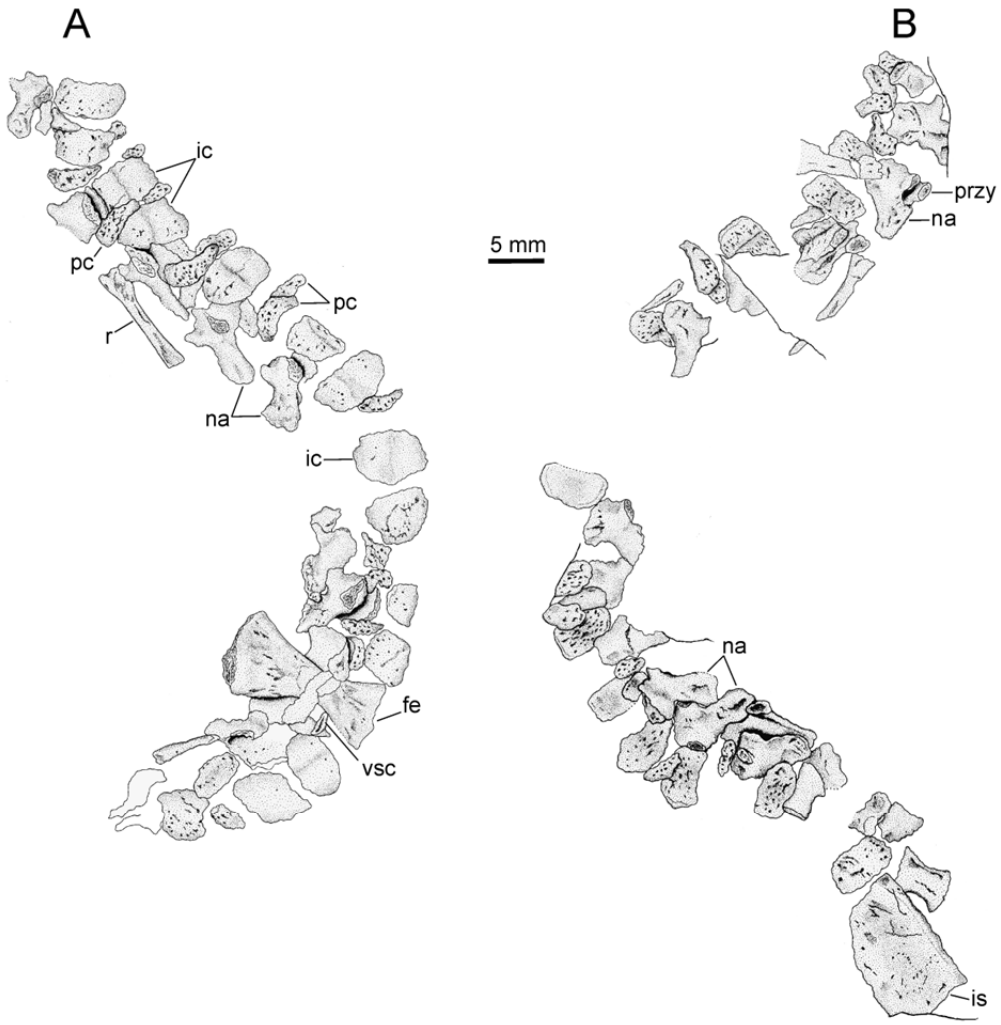

Figure 8 *Acanthostomatops vorax*. Vertebral column of the largest specimen LFUG-13244+45 (75 mm): (A) LFUG-13244, ventral, with femur; (B) LFUG-13245, dorsal, with ischium.

determined (Figs 6D, 10C). The present new orientation gives the roughly triangular ornamented field a more familiar outline, with the pointed end facing anteriorly, a condition established in many dissorophoids. A posterior process is not developed, and the anterior margin is not serrated. As indicated by the overlap facets, the clavicular blades overlapped the interclavicle far medially but did not meet in the ventral midline. In branchiosaurids, where the interclavicle is similarly small, there is only a short overlap of the clavicles (Boy 1972). The dorsal surface is slightly convex and largely smooth, except for the parts dorsal to the clavicular facets which are raised and bear radially aligned striations. A semilunar ridge, which is so typical of many temnospondyls, is not established on the dorsal side.

Clavicles. The clavicles are also known only in small specimens. Again as in dissorophoids, the clavicular blades are very slender (LFUG-13227, 13523, 13566) and their ventral surface is ornamented by ridges and furrows (Figs 6D, 7, 10C). However, the shaft (prescapular process) is peculiar in being very slender and much longer than in larval *Sclerocephalus* (Schoch 2003), *Archegosaurus* (Witzmann & Schoch in press) and *Onchiodon* (Witzmann 2005). Its medial side bears a broad groove bordered anteriorly by a bulge, where the slender shaft of the cleithrum was set in. Obviously, only the dorsal head of the cleithrum extended above the clavicle, which is a rather unusual situation among temnospondyls.

Cleithra. The cleithra are adequately preserved only in very small specimens (LFUG-13417, 13229; Fig. 6A, B) and in the largest individual (LFUG-13244+45; Fig. 10D, E). The slender element bears an asymmetrical dorsal head with the posterior portion being longer than the anterior part. In LFUG-13229, the head ends in a pronounced dorsal outgrowth. Throughout ontogeny, the head of the cleithrum is proportionally smaller and much more slender than in *Onchiodon* (Witzmann 2005), *Sclerocephalus* (Schoch 2003; Meckert 1993) and dissorophids (Berman *et al.* 1985). In LFUG-13244, almost the complete cleithrum is preserved in medial view and the cleithral head in lateral view on the counterslab LFUG-13245. Compared with the taxa cited above, the head lacks posterior extension dorsal to the scapulocoracoid. The lateral side of the head is convex and bears radially aligned grooves anterolaterally. On the medial side, it is divided by a crest that continues onto the dorsal half of the shaft. This forms the articulation facet for the scapulocoracoid.

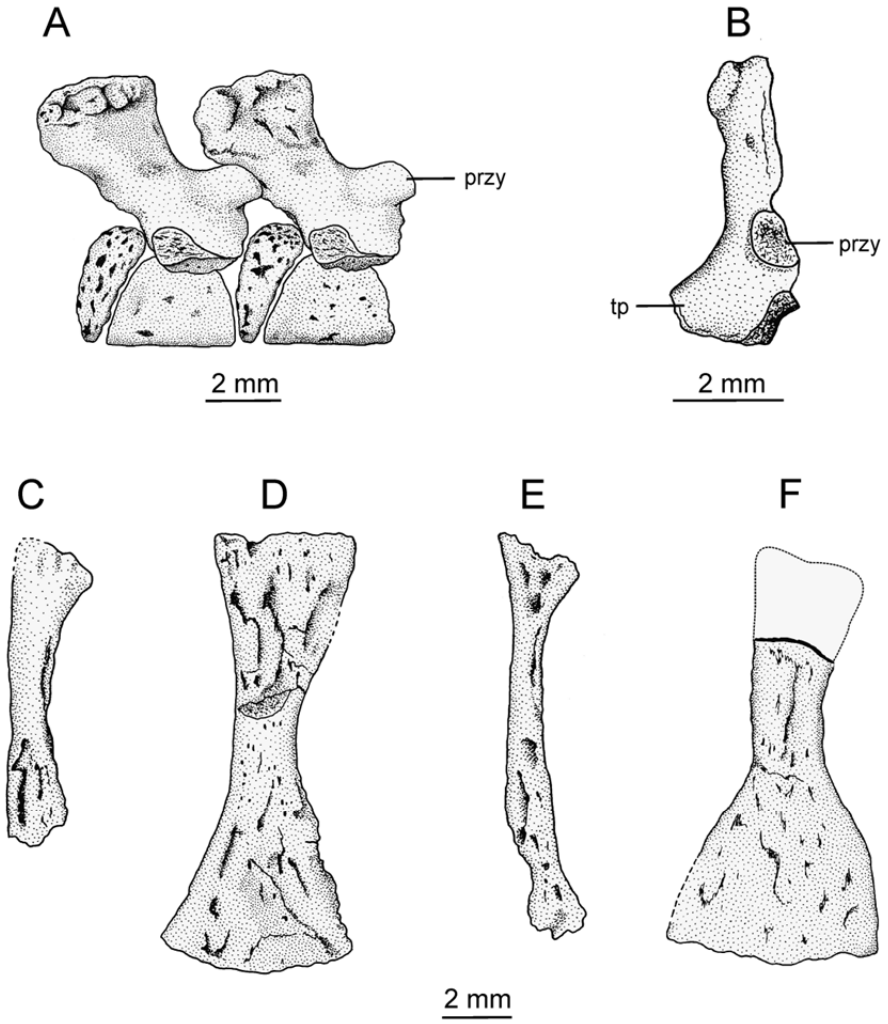

Figure 9 *Acanthostomatops vorax*. (A) reconstruction of vertebrae based on LFUG-13244+45 in lateral view; (B) LFUG-13244, right portion of neural arch in anterior view; (C)–(F) ribs of LFUG-13244+45: (C) first rib; (D) thoracal rib; (E) rib from the posterior half of the trunk; (F) sacral rib.

Scapulocoracoid. The smallest specimen with ossified parts of the scapulocoracoid is 19 mm long MB.Am.411. However, Steen's (1937, pl. 2, figs 2–3) 'specimen A' (15 mm) preserved the clear-cut outlines of the scapulocoracoid. Further specimens are LFUG-13522+23 (Fig. 6C, D), MMG-SaP-130, and 131. Throughout the sample, the element forms a rather short, semilunar plate with ill-defined margins that is substantially shorter than the humerus.

3.7.3. Forelimb. *Humerus*. Again, this bone is preserved only in specimens of small and intermediate size (LFUG-13229, 13523, MMG-SaP-130, 131, 743). As compared to the short, very rudimentary humeri of larval *Sclerocephalus* (Boy 1972; Schoch 2003), *Archegosaurus* (Witzmann & Schoch in press), and *Onchiodon* (Witzmann 2005), that of *Acanthostomatops* is much more complete and robust at comparable stages. By 15 mm skull length, it is already well differentiated (Fig. 11A), with fairly complete ends (LFUG-13229 and Steen's 'specimen A'). The humerus is clearly waisted, with the shaft being proportionally more slender and longer than in the above-listed temnospondyls. The proximal head is more expanded and massive than the distal end. In 36 mm MMG-SaP-130 the humerus has a deltopectoral crest and a tiny supinator process (Fig. 11C), while 38 mm MMG-SaP-743 (Fig. 11B) preserves the humerus in its three-dimensional shape, suggesting a near-perfect tetrahedral structure with proximal and distal ends being aligned at an angle of nearly 90°. Interestingly, the humerus is longer than the femur in specimens beyond about 30 mm skull length, a unique feature amongst temnospondyls. In smaller specimens, however, the femur is longer than the humerus (see below).

Radius and ulna. These bones are adequately preserved only in LFUG 13566 (Fig. 11D) and MMG-SaP-130 (Fig. 11C). They reach somewhat more than half the length of the humerus. The ulna is slightly longer than the radius, but an olecranon process is not present. The element is more expanded proximally than distally. The radius is distally broader than the ulna.

Manus. The manus is not completely preserved in any specimen. It is exposed in LFUG 13566 (Fig. 11D), where the following phalangeal formula was derived: ?2–?2–3–?3. Provided this to be the correct count, it would be identical with that of *Onchiodon labyrinthicus* (Witzmann 2005). The

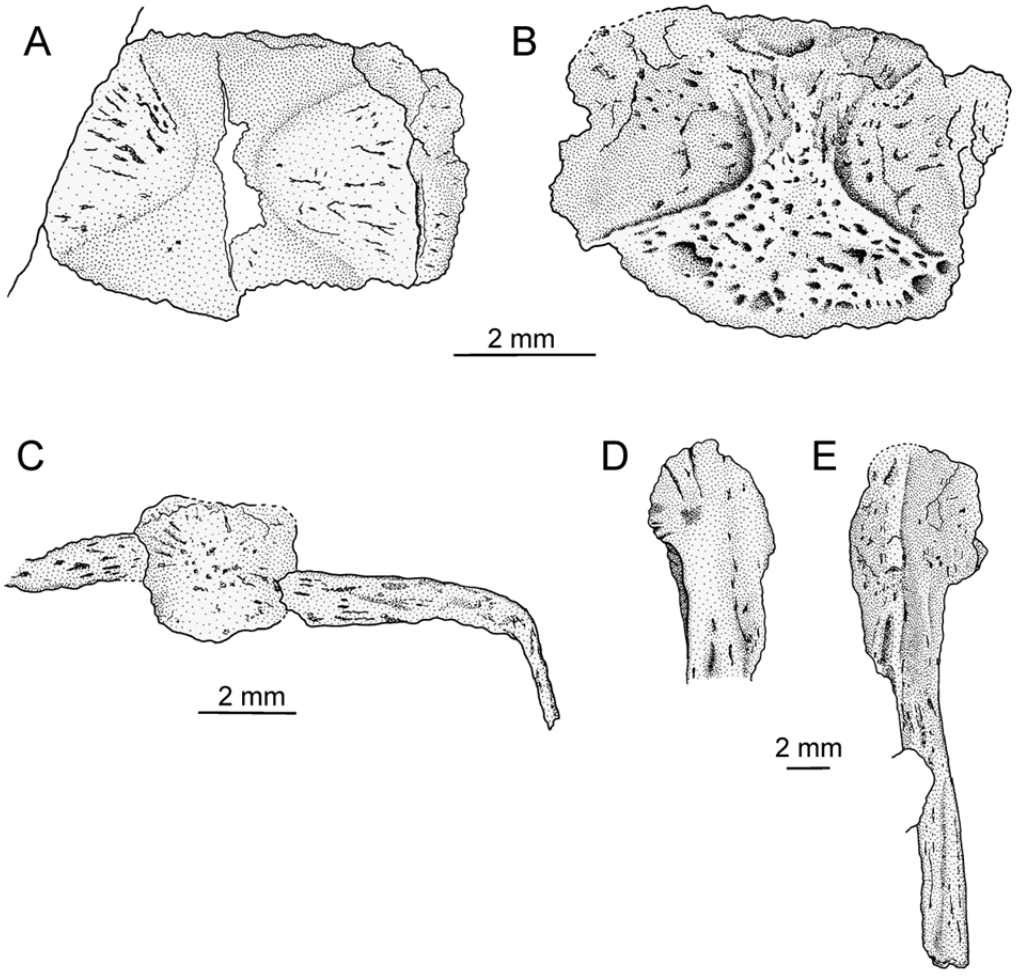

Figure 10 *Acanthostomatops vorax*. Elements of the dermal pectoral girdle: (A), (B) LFUG-13566+67, circa 32 mm, interclavicle: (A) dorsal; (B) ventral; (C) LFUG-13227, 20 mm, ventral, interclavicle and clavicles; (D), (E) LFUG-13244+45 (75 mm) cleithrum: (D) lateral; (E) medial.

terminal phalanges consist of short, blunt claws. There are no carpal bones.

3.7.4. Pelvic girdle. In the pelvic girdle, the ilium and ischium have been found in different size stages, whereas the pubis is not preserved. Ilium and ischium are not co-ossified in any specimen.

Ilium. By 17 mm skull length (LFUG-13221), the ilium is the only ossified element of the pelvic girdle (Fig. 12A). Dorsal to the small triangular base, the iliac blade is stout, low and almost rectangular in lateral view, being only slightly expanded dorsally. In LFUG-13566+67, it is more differentiated, having a well-established dorsal frame to the acetabulum and a shaft with an expanded dorsal portion (Fig. 7). In LFUG-13245, the ilium is rather robust with a large and rounded-triangular base (Fig. 12C). The dorsal rim of the acetabulum has an irregular outline and is expanded posterodorsally, and the bone surface of the acetabulum is markedly rugose. The broad, probably vertically aligned shaft resembles that of *Eryops* (Romer 1922) and *Onchiodon* (Romer 1925; Boy 1990), although in the latter it is even more expanded at the dorsal end. A ventral shelf that must have attached to the ischium is preserved; its greatest extension is at about mid-level of the acetabulum and continues to a point well anterior to it. This indicates either a markedly anterior extension of the ischium, or alternatively the existence of a pubic ossification at this size stage.

Ischium. The ischium formed clearly after the ilium, by 32 mm skull length (LFUG-13566+67; Fig. 7). At this size, it is still shorter than the base of the ilium. The outline is trapezoidal with the anterior and posterior margins being almost straight. Its anterior portion is deeper and thicker than the posterior part. While the dorsal portion is laterally convex, the ventrolateral portion has a concave surface. In LFUG-13245, the crescent-shaped ischium is proportionally larger, and the anterior margin has a bulbous surface (Fig. 8B). In the posterior half, the lateral surface is concave, while the posterior end has a convex, thickened margin.

3.7.5. Hindlimb. ***Femur***. LFUG-13229 preserves both the humerus (Fig. 11A) and the femur (Fig. 6B) permitting a size comparison between them. There, the femur is about 1·7 times longer than the humerus. (Confusingly, Steen 1937, fig. 3 referred to the femur as the humerus in this specimen). In LFUG-13229, the femur has a moderately long and slender shaft and a pronounced adductor crest, and it is about 1·8 times longer than the fibula in LFUG-13221 (Fig. 12A).

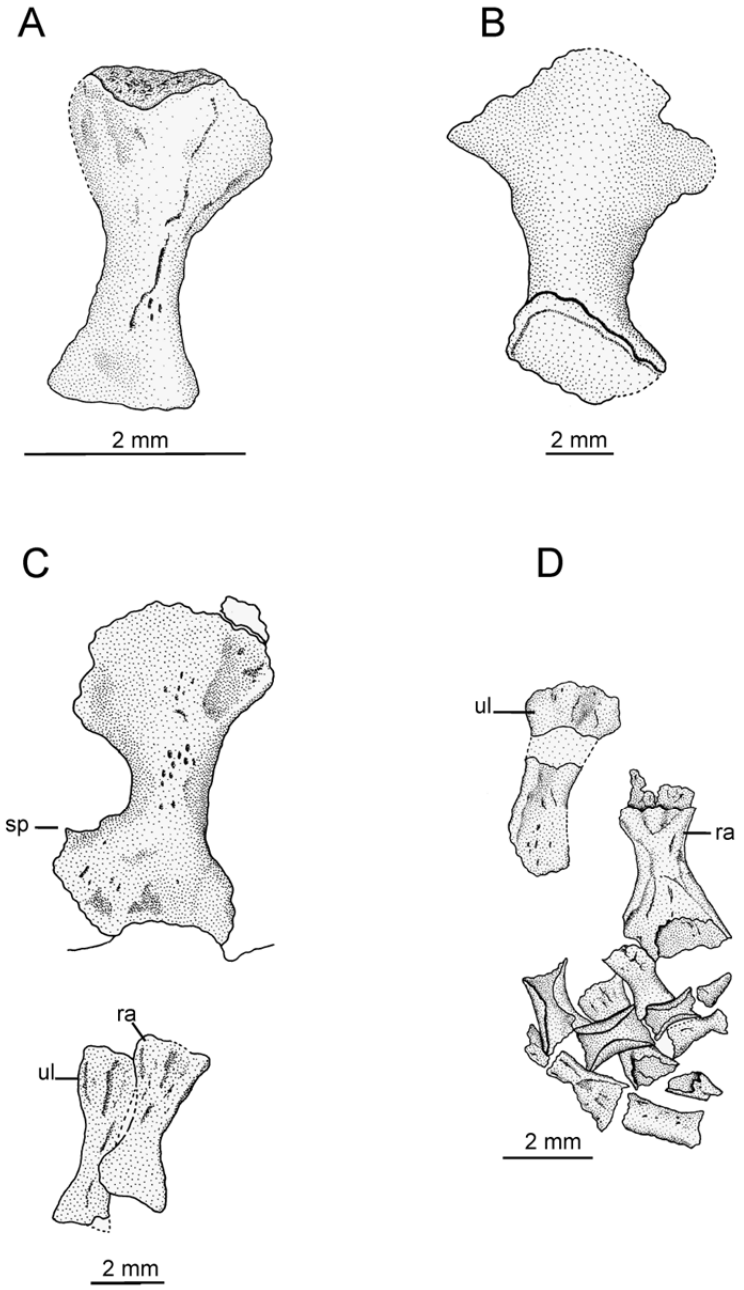

Figure 11 *Acanthostomatops vorax*. Forelimbs: (A) LFUG-13229, 15 mm, humerus; (B) MMG-SaP-743, 38 mm, humerus; (C) MMG-SaP-130, 36 mm, humerus, radius, and ulna; (D) LFUG-13566, circa 32 mm, radius, ulna, and manus.

During later ontogeny, the femur reveals a negative allometry with respect to skull length (LFUG-12566+67; Fig. 7), and in the largest specimen LFUG-13244 it is massive and strikingly short (Fig. 12B). The clearly two-headed distal end is 1.3 times wider than the proximal end. The shaft is narrowest in the proximal third of the bone. In the large specimen, the adductor crest is knife-edged but proportionally lower than in LFUG-13229.

Tibia and fibula. These bones can already be distinguished in small specimens (e. g. LFUG-13221; Fig. 12A). The tibia is slightly shorter than the fibula and has a more expanded proximal head compared to the distal end. The fibula has a pronounced, enlarged distal end that is angled medially. Its lateral and medial margins are clearly concave. In a larger specimen (LFUG-13566; Fig. 7), the fibula is overall more slender and the lateral margin less concave.

Pes. LFUG-13566+67 is the only specimen in which the foot is adequately preserved, and was figured by Boy (1989, fig. 5c). The present authors suggest that the phalangeal formula probably reads: ?2–**2**–3–4–?3 rather than ?2–**?3**–3–?4–3 as

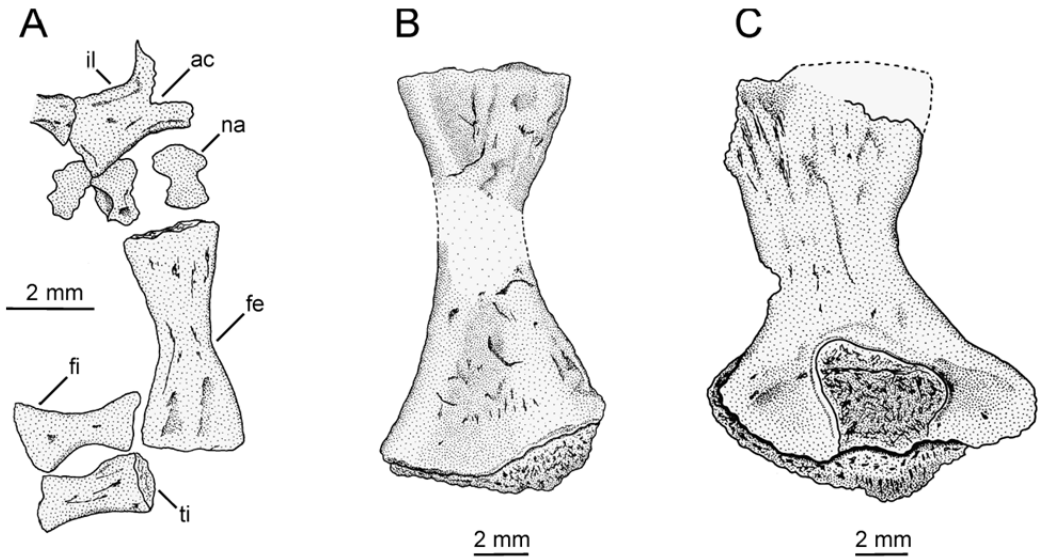

Figure 12 *Acanthostomatops vorax*. (A) LFUG-13221, 17 mm, ilium, femur, tibia and fibula; (B) LFUG-13244, 75 mm, femur; (C) LFUG-13245, 75 mm, ilium.

proposed by Boy (1989). The terminal phalanges are short and pointed (Fig. 7). There is no evidence of ossified tarsals.

3.7.6. Dermal scales. Steen (1937, p. 498) reported 'a patch of very delicate scaling' in the small 'specimen A' with a skull length of approximately 15 mm. Although it is not clear if these were rounded-oval dorsal or spindle-shaped ventral scales, this observation shows that the dermal scales started to ossify early in larval ontogeny. By 32 mm skull length (LFUG-13566; Fig. 7), spindle-shaped scales with a convex ventral and concave dorsal margin are preserved that were arranged in a V-pattern on the ventral side of the trunk in the living animal. An isolated scale of this type is also preserved in the largest specimen (LFUG 13245; Fig. 8A). Dorsal scales are not preserved.

4. Discussion

Boy (1989) split the 24 specimens of *Acanthostomatops vorax* investigated by him into four ontogenetic phases which he referred to as 'larval' (smaller than 20 mm skull length), 'metamorphosing' (20–30 mm), 'juvenile' (30–60 mm), and 'adult' (beyond 60 mm) respectively. Boy's concept of ontogenetic phases including the metamorphic phase is based exclusively on developmental changes in ornamentation, by analogy to his findings in *Sclerocephalus* (Boy 1988). However, such changes in ornamentation alone do not form sufficient evidence for a metamorphosis in most temnospondyls (Schoch 2001).

4.1. Hyobranchial remodelling

Boy & Sues (2000) and Schoch (2001) suggested that the resorption of branchial denticles may be an important criterion for metamorphosis in temnospondyls because it indicates the remodelling of ceratobranchials in analogy to extant salamanders. However, the lack of branchial dentition in *Acanthostomatops*, makes the recognition of any metamorphic phase difficult. One possibility is to consider the probable resorption of ossified ceratobranchials as a metamorphic event (Schoch 2002). In *Onchiodon*, this event occurred more or less simultaneously with the resorption of branchial denticles (Witzmann 2005). In *Acanthostomatops*, there are no ossified ceratobranchials preserved in specimens larger than 22 mm skull length. This suggests their resorption between 20 and 30 mm, thus corroborating nicely the metamorphic phase in Boy's (1989) model.

The large specimen LFUG-13244+45 lacks any ceratobranchials. Instead, it preserves a full range of rather different, mostly straight and delicate elements in the anterior part of the parasphenoid plate, at about the level where an 'adult' hyobranchial skeleton is to be expected. Morphologically, the long bony rods match the hypobranchials most closely. If this interpretation is correct, then large *Acanthostomatops* had a total of four pairs of ossified hypobranchials, in contrast to trimerorhachoids, dissorophoids, and most extant salamanders, in which only two such pairs are or were ossified (Bystrow 1938; Boy & Sues 2000). More than two pairs occur also in lysorophians (four pairs, Wellstead 1991), adelogyrinids (three pairs, Andrews & Carroll 1991), and the tristichopterid sarcopterygian *Eusthenopteron* (Jarvik 1980), which may indicate the plesiomorphic state. The nature of the short rods and plate-like bones in the vicinity of the possible hypobranchials of LFUG-13244 is unclear; they could either form segments of the hyoid arch or alternatively represent medial ossifications in the basibranchial region.

In sum, the larval hyobranchial apparatus was probably reorganised in specimens beyond 22 mm skull length, starting with the resorption of ceratobranchials. In the adult hyobranchium, only the anteroventral portion of the skeleton was ossified. Thus, in *Acanthostomatops* a 'larval' gill-supporting skeleton apparently transformed into an 'adult' tongue-supporting apparatus. By analogy with extant salamanders, this 'adult' hyobranchial apparatus might have served a tongue-supporting function that assisted in prey capture. This fits into the concept that in zatracheids, an enlarged intermaxillary gland played a key role in terrestrial feeding (Schoch 1997).

4.2. Life history of *Acanthostomatops*

Biphasic life-cycles where there is a shift from an aquatic to a terrestrial mode of life are difficult to prove in the fossil record.

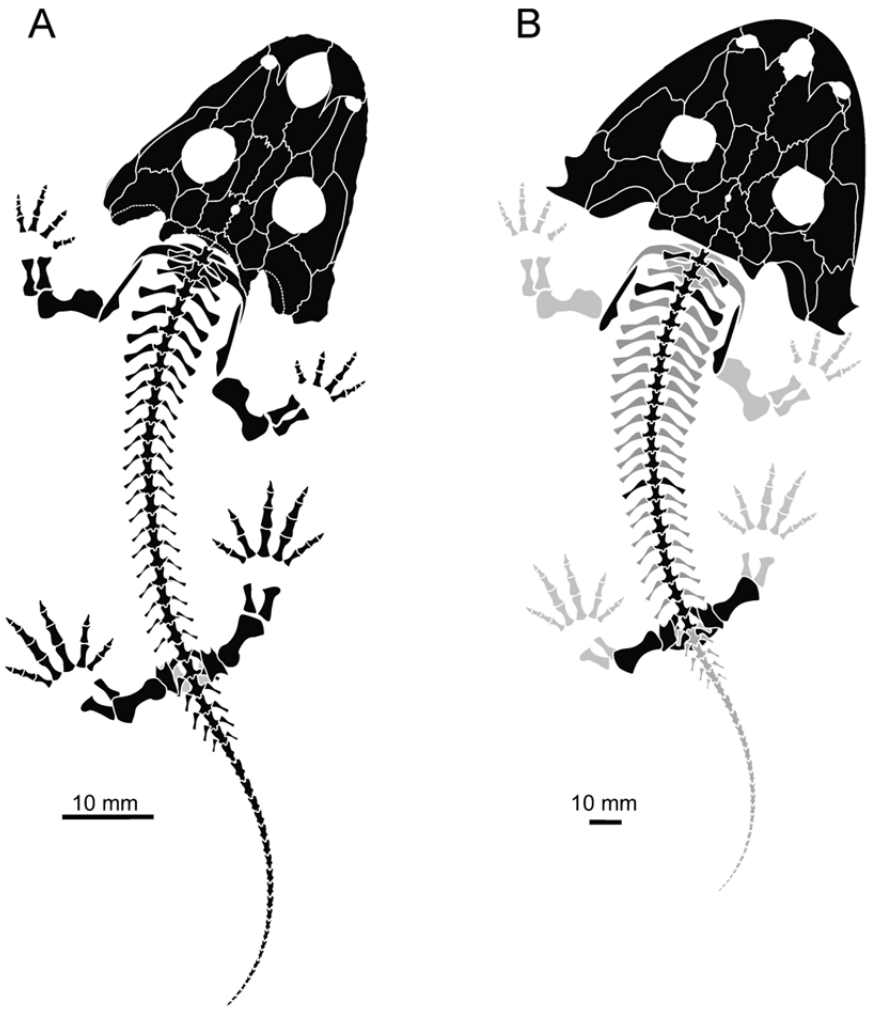

Figure 13 *Acanthostomatops vorax*. Reconstructions of complete skeletons in dorsal view: (A) early juvenile skeleton, based on several specimens; (B) adult specimen, based on LFUG-13244+45; unknown parts of the skeleton are shown in grey.

Boy (1989) and Schoch (2002) assumed such a transition during life history of *Acanthostomatops*, following Paton (1975) who regarded the adults of the zatracheids *Dasyceps* and *Zatrachys* as terrestrial forms.

4.2.1. Larvae. Specimens smaller than 25–30 mm skull length probably lived as aquatic larvae in the Niederhäslich lake. Their possession of ossified ceratobranchials is a larval adaptation. These ceratobranchials probably supported external gills and stiffened the gill clefts. (The lack of any external gills in the Niederhäslich material is in agreement with the lack of any skin preservation, except for ossified scales.) An aquatic mode of life is also supported by the poorly ossified postcranial skeleton. On the other hand, the smallest known specimens already have features that foreshadow a terrestrial mode of life realised in adult ontogeny. These include having a well-developed, differentiated humerus, a femur with a distinct adductor crest, the small dermal elements in the pectoral girdle, the nasolacrimal duct, and the proportionally short bony tail. The large intervomerine fontanelle is already well defined, which is believed to have housed an intermaxillary gland used in terrestrial feeding (Schoch 1997). In larvae, the proportionally larger size of the hindlimb and the longer trunk suggest an active mode of swimming, probably by lateral undulation of the axial skeleton and a support in steering by the hindlimb.

4.2.2. Juveniles. Specimens in the 30–60 mm skull size range probably still lived in the water. This is suggested by the high frequency of specimens in that size range as indicated by the size distribution given in Figure 1A. The still feebly ossified postcranial skeletons, especially the unossified vertebral centra, still missing carpals and tarsals, and the low degree of ossification of scapulocoracoid and pelvis, suggest these animals were not capable of an entirely terrestrial existence. Boy (1989) supposed that the juveniles lived probably as semi-aquatic animals in the shallow littoral zone. The slow ossification of the postcranial skeleton in *Acanthostomatops* is shared with *Onchiodon* (Boy 1990; Witzmann 2005) and *Sclerocephalus* (Boy 1988; Schoch 2003), but stands in stark contrast to the rapid ossification in dissorophoids. A restoration of a juvenile skeleton is shown in Figure 13A.

4.2.3. Adults. The ossification of the vertebral centra, which must have occurred in specimens of between 45 mm and 75 mm skull length, marks an important change. With its huge skull and the short trunk and limbs, an adult

Acanthostomatops was rather stout, quite similar to the extant leptodactylid frog *Ceratophrys*. Like *Ceratophrys*, it may well have been a rather passive terrestrial predator that lurked for passing prey. In such a situation, a projectable tongue might have been an advantage; the peculiar adult tongue skeleton of *Acanthostomatops* may shed some light on this topic. Although the humerus, carpals and tarsals, and scapulocoracoid are not preserved in the adult specimen, there are some novel 'adult' features suggesting a terrestrial life. These are the proportionally large zygapophyses that probably strengthened the vertebral column in supporting the animal on land, the proportionally large ischium with its sutural connection to the ilium, the robust and vertical iliac blade, and the general absence of lateral lines. Furthermore, there is some admittedly weak evidence for the existence of a pubic ossification. The terrestrial life of adult *Acanthostomatops* is also supported by the size distribution of the material studied by the present authors: It shows that large juveniles and adults are very rare. Boy & Sues (2000) interpreted this as a result of departure from the aquatic habitat. A reconstructed adult skeleton is illustrated in Figure 13B.

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6. Abbreviations used in figures

ac—acetabulum
adc—adductor crest
al—ascending lamella
bf—basioccipital fossa
bp-ar—facet for basipterygoid articulation
bp-pr—basipterygoid process
car-f—exit foramina for the internal carotid
ce-br—ceratobranchials
cho—choana
cl—clavicle
cr-po—paroccipital crest
cr-pp—parapterygoid crest
cr-sc—crista sellaris
ct—cleithrum
den—denticle field
ec—ectopterygoid
f—frontal
fe—femur
fi—fibula
fon—internasal fontanelle
fp—footplate
ha—haemal arch
hu—humerus
hy—hyobranchial element
hy-br—hypobranchials
ic—intercentrum
icl—interclavicle
il—ilium
is—ischium
j—jugal
la—lacrimal
m—maxilla
mp—muscular pocket
n—nasal
na—neural arch
of—occipital flange
p—parietal
pc—pleurocentrum
pi—pineal foramen
pl—palatine
pm—premaxilla
po—postorbital
pof—postfrontal
pos—palatal ossicles
pp—postparietal
prat—proatlas
prf—prefrontal
przy—prezygapophyses
ps-cu—cultriform process of parasphenoid
ps-pl—parasphenoid plate
pt—pterygoid
q—quadrate
qj—quadratojugal
r—rib
ra—radius
sc—scapulocoracoid
sm—septomaxilla
sp—supinator process
spp—socket for parotic process
sq—squamosal
sr—sacral rib
st—supratemporal
stap—stapes
t—tabular
ti—tibia
tp—transverse process
ul—ulna
v—vomer
v-fon—vomerine fontanelle
vp—ventral process
vsc—ventral scale

7. References

Andrews, S. M. & Carroll, R. L. 1991. The order Adelospondyli: Carboniferous lepospondyl amphibians. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **82**, 239–275.

Berman, D. S., Reisz, R. R. & Eberth, D. A. 1985. *Ecolsonia cutlerensis*, an Early Permian dissorophid amphibian from the Cutler Formation of North-Central New Mexico. *New Mexico Bureau of Mines & Mineral Resources: Circular* **191**, 5–31.

Bolt, J. R. & Lombard, R. E. 1985. Evolution of the amphibian tympanic ear and the origin of frogs. *Biological Journal of the Linnean Society* **24**, 83–99.

Boy, J. A. 1972. Die Branchiosaurier (Amphibia) des saarpfälzischen Rotliegenden (Unter-Perm, SW-Deutschland). *Abhandlungen des hessischen Landesamts für Bodenforschung* **65**, 1–137.

Boy, J. A. 1974. Die Larven der rhachitomen Amphibien (Amphibia: Temnospondyli; Karbon-Trias). *Paläontologische Zeitschrift* **48**, 236–248.

Boy, J. A. 1985. Über *Micropholis*, den letzen Überlebenden der Dissorophoidea (Amphibia, Temnospondyli; Unter-Trias). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1985**, 29–45.

Boy, J. A. 1988. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstes Karbon-Perm) 1. *Sclerocephalus*. *Paläontologische Zeitschrift* **62**, 107–132.

Boy, J. A. 1989. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstes Karbon-Perm) 2. *Acanthostomatops*. *Paläontologische Zeitschrift* **63**, 133–151.

Boy, J. A. 1990. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?höchstes Karbon-Perm) 3. *Onchiodon*. *Paläontologische Zeitschrift* **64**, 287–312.

Boy, J. A. 1995. Über die Micromelerpetontidae (Amphibia: Temnospondyli). 1. Morphologie und Paläoökologie des *Micromelerpeton credneri* (Unter-Perm; SW-Deutschland). *Paläontologische Zeitschrift* **69**, 429–457.

Boy, J. A. & Sues, H.-D. 2000. Branchiosaurs: Larvae, Metamorphosis and Heterochrony in Temnospondyls and Seymouriamorphs. *In* Heatwole, H. & Carroll, R. L. (eds) *Amphibian Biology 4: Palaeontology*, 1150–97. Chipping Norton: Surrey Beatty.

Bystrow, A. P. 1938. *Dvinosaurus* als neotenische Form der Stegocephalen. *Acta Zoologica* **19**, 209–95.

Bystrow, A. P. & Efremov, I. A. 1940. *Benthosuchus sushkini* Efremov. A labyrinthodont from the Eotriassic of Sharzenga River. *Travaux de l'institut paléontologique académie de sciences de l'USSR* **10**, 1–152. [In Russian with English summary.]

Carroll, R. L. 1964. Early evolution of the dissorophid amphibians. *Bulletin of the Museum of Comparative Zoology, Harvard University* **131**, 161–250.

Case, E. C. 1911. Revision of the Amphibia and Pisces of the Permian of North America. *Publications of the Carnegie Institute Washington* **146**, 1–179.

Case, E. C. 1935. Description of a collection of associated skeletons of *Trimerorhachis*. *Contributions of the Museum of Paleontology at the University of Michigan* **4**, 227–74.

Chase, J. N. 1965. *Neldasaurus wrightae*, a new rhachitomous labyrinthodont from the Texas Lower Permian. *Bulletin of the Museum of Comparative Zoology, Harvard University* **133**, 153–225.

Clack, J. A. & Milner, A. R. 1994. *Platyrhinops* from the Upper Carboniferous of Linton and Nýřany and the family Amphibamidae (Amphibia: Temnospondyli). *In* Heidtke, U. (ed.) *New Research on Permo-Carboniferous Faunas. Pollichia-Buch* **29**, 185–91.

Cope, E. D. 1882. The rhachitomous Stegocephalia. *American Naturalist* **16**, 334–5.

Credner, H. 1881. Die Stegocephalen aus dem Rothliegenden des Plauen'schen Grundes bei Dresden. Erster Theil. *Zeitschrift der deutschen geologischen Gesellschaft* **33**, 298–330.

Credner, H. 1883. Die Stegocephalen aus dem Rothliegenden des Plauen'schen Grundes bei Dresden. Vierter Theil. *Zeitschrift der deutschen geologischen Gesellschaft* **35**, 275–300.

Daly, E. 1994. The Amphibamidae (Amphibia: Temnospondyli), with a description of a new genus from the Upper Pennsylvanian of Kansas. *University of Kansas Museum of Natural History, Miscellaneous Publications* **85**, 1–59.

Geinitz, H. B. & Deichmüller, J. V. 1882. Die Saurier der unteren Dyas von Sachsen. *Palaeontographica* **29**, 1–46.

Holmes, R. B., Carroll, R. L. & Reisz, R. R. 1998. The first articulated skeleton of *Dendrerpeton acadianum* (Temnospondyli, Dendrerpetontidae) from the Lower Pennsylvanian locality of Joggins, Nova Scotia, and a review of its relationships. *Journal of Vertebrate Paleontology* **18**, 64–79.

Hotton, N. III. 1959. *Acroplous vorax*, a new and unusual labyrinthodont amphibian from the Kansas Permian. *Journal of Paleontology* **33**, 161–78.

Jarvik, E. 1980. *Basic structure and evolution of vertebrates*, Vol. 1. London: Academic Press.

Kuhn, O. 1961. *Die Familien der rezenten und fossilen Amphibien und Reptilien*. Bamberg: Meisenbach-Verlag.

Langston, W. 1953. Permian amphibians from New Mexico. *University of California Publications in Geological Sciences* **29**, 349–416.

Mazin, J.-M. & Janvier, P. 1983. L'anatomie de *Lyrocephaliscus euri* (Wiman), trématosaure du Trias inférieur du Spitsberg: arrière crâne, squellete axial et ceinture scapulaire. *Palaeovertebrata* **13**, 13–31.

Meckert, D. 1993. Der Schultergürtel des *Sclerocephalus haeuseri* Goldfuss, 1847 im Vergleich mit *Eryops* Cope, 1877 (Eryopoidea, Amphibia, Perm). *Palaeontographica* **A229**, 113–40.

Milner, A. R. & Sequeira, S. 1998. A cochleosaurid temnospondyl amphibian from the Middle Pennsylvanian of Linton, Ohio, USA. *Zoological Journal of the Linnean Society* **122**, 261–90.

Olson, E. C. 1979. Aspects of the biology of *Trimerorhachis* (Amphibia: Temnospondyli). *Journal of Paleontology* **53**, 1–17.

Paton, R. L. 1975. A Lower Permian temnospondylous amphibian from the English Midlands. *Palaeontology* **18**, 831–45.

Romer, A. S. 1922. The locomotor apparatus of certain primitive and mammal-like reptiles. *Bulletin of the American Museum of Natural History* **10**, 517–606.

Romer, A. S. 1925. Permian amphibian and reptilian remains described as *Stephanospondylus*. *Journal of Geology* **33**, 447–63.

Säve-Söderbergh, G. 1936. On the morphology of Triassic stegocephalians from Spitsbergen, and the interpretation of the endocranium in the Labyrinthodontia. *Kunglik Svensk Vetenskapsakademiens Handlingar* **16**, 1–181.

Sawin, H. J. 1941. The cranial anatomy of *Eryops megacephalus*. *Bulletin of the Museum of Comparative Zoology at Harvard College* **88**, 407–63.

Schneider, J. 1994. Environment, biotas and taphonomy of the Lower Permian lacustrine Niederhäslich limestone, Döhlen Basin, Germany. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **84** (for 1993), 453–64.

Schoch, R. R. 1997. Cranial anatomy of the Permian temnospondyl amphibian *Zatrachys serratus* Cope 1878, and the phylogenetic position of the Zatracheidae. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **206**, 223–48.

Schoch, R. R. 2000. The stapes of *Mastodonsaurus giganteus* (Jaeger 1828) – structure, articulation, ontogeny, and functional implications. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **215**, 177–200.

Schoch, R. R. 2001. Can metamorphosis be recognised in Palaeozoic amphibians? *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **220**, 335–67.

Schoch, R. R. 2002. The evolution of metamorphosis in temnospondyls. *Lethaia* **35**, 309–27.

Schoch, R. R. 2003. Early larval ontogeny of the Permo-Carboniferous temnospondyl *Sclerocephalus*. *Palaeontology* **46**, 1055–72.

Schoch, R. R. 2006. A new trematosaurid from the Middle Triassic of Germany. *Journal of Vertebrate Paleontology* **26**, 29–43.

Schoch, R. R. & Milner, A. R. 2004. Structure and implications of theories on the origin of lissamphibians. *In* Arratia, G., Wilson, M. V. H. & Cloutier, R. (eds) *Recent advances in the origin and early radiation of vertebrates*, 345–77. Munich: Verlag Dr. Friedrich Pfeil.

Shishkin, M. A. 1973. The morphology of the early Amphibia and some problems of lower tetrapod evolution. *Trudy Paleontologiceskogo Instituta Akademiya Nauk SSSR* **137**, 1–257. [In Russian.]

Shishkin, M. A., Rubidge, B. S. & Kitching, J. W. 1996. A new lydekkerinid (Amphibia, Temnospondyli) from the lower Triassic of South Africa: implications for evolution of the early capitosaurid cranial pattern. *Philosophical Transactions of the Royal Society London* **B351**, 1635–59.

Steen, M. C. 1937. On *Acanthostoma vorax* Credner. *Proceedings of the Zoological Society London* **B107**, 491–500.

Sushkin, P. 1927. On the modifications of the mandibular and hyoid arches and their relations to the brain-case of the early Tetrapoda. *Paläontologische Zeitschrift* **8**, 263–321.

Van Hoepen, E. C. N. 1915. Stegocephalia of Senekal, O. F. S. *Annals of the Transvaal Museum* **5**, 124–49.

Wellstead, C. F. 1991. Taxonomic revision of the Lysorophia, Permo-Carboniferous lepospondyl amphibians. *Bulletin of the American Museum of Natural History* **209**, 1–90.

Werneburg, R. 1998. Ein larvaler *Acanthostomatops* (Zatrachydidae, Amphibia) aus der Niederhäslich-Formation (Unter-Perm) des Döhlen-Beckens. *Veröffentlichungen des Museums für Naturkunde Chemnitz* **21**, 49–52.

Witzmann, F. 2005. Hyobranchial and postcranial ontogeny of the temnospondyl *Onchiodon labyrinthicus* (Geinitz, 1861) from Niederhäslich (Döhlen Basin, Autunian, Saxony). *Paläontologische Zeitschrift* **79**, 479–92.

Witzmann, F. & Schoch, R. R. In press. The postcranium of *Archegosaurus decheni*, and a phylogenetic analysis of temnospondyl postcrania. *Palaeontology*.

Yates, A. & Warren, A. A. 2000. The phylogeny of the 'higher' temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. *Zoological Journal of the Linnean Society* **128**, 77–121.

Zittel, K. A. R. v. 1888. *Handbuch der Palaeontologie: I. Abtheilung. Palaeozoologie. Vol. III. Vertebrata* (*Pisces, Amphibia, Reptilia, Aves*). Berlin: R. Oldenbourg.

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